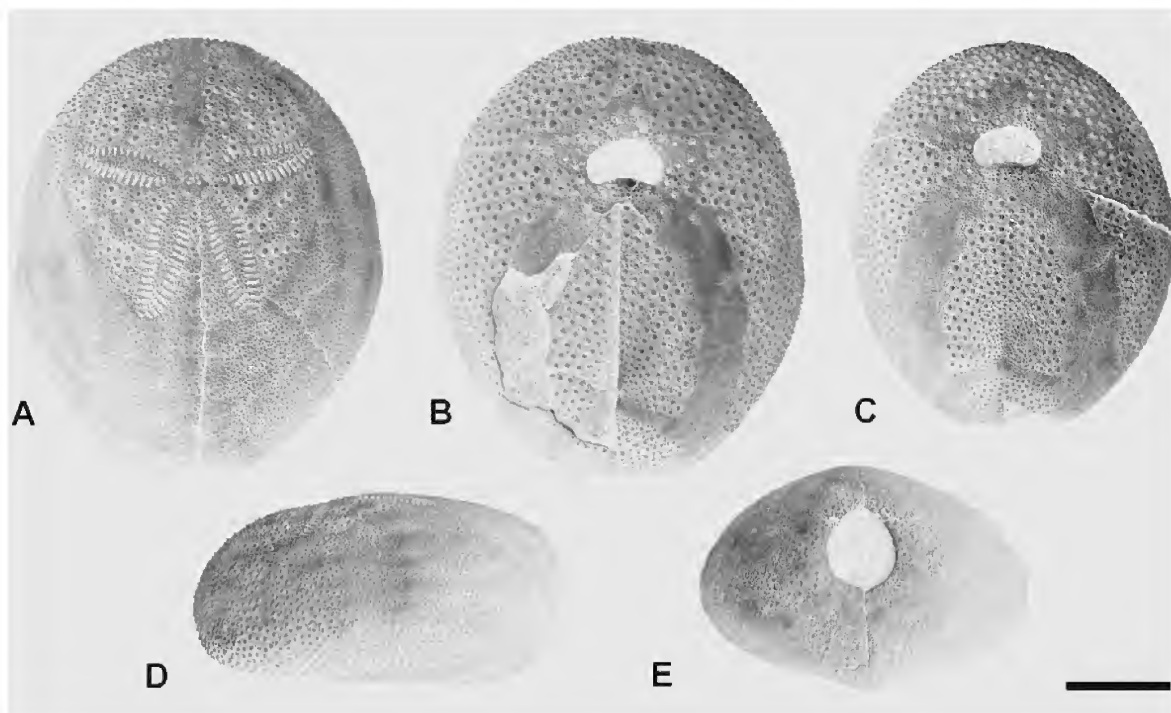
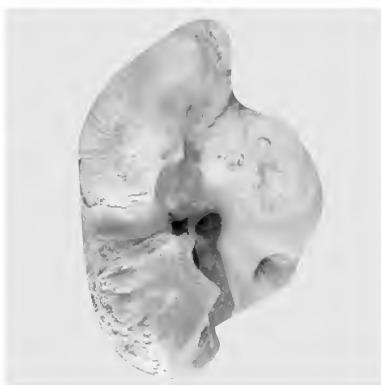
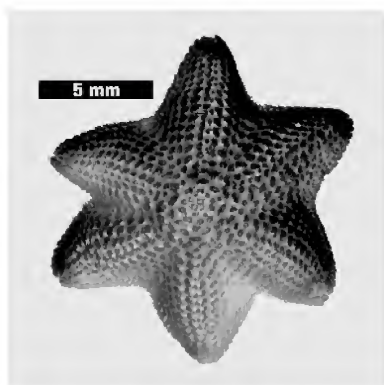


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*Front cover* Top left: a new species of seastar from Mauritius, *Ailsastra eleaumei*, described by P. Mark O'Loughlin and Francis W.E. Rowe. Top centre: an earbone of a fossil dolphin of the family Delphinidae from the Pliocene Whalers Bluff Formation, Portland, Victoria, described by Erich M. G. Fitzgerald. Bottom: a new species of fossil sea urchin, *Spatagobrissus dermodyorum*, described by Francis Holmes from the early Middle Miocene Glenforslan Formation near Blanchetown, South Australia. Back cover: male reproductive organs of a new species of millipede, *Lissodesmus dignomontis*, from Tasmania, described by Robert Mesibov.

## The millipede genus *Lissodesmus* Chamberlin, 1920 (Diplopoda: Polydesmida: Dalodesmidae) from Tasmania and Victoria, with descriptions of a new genus and 24 new species

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### Abstract

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*Lissodesmus* includes *L. adrianae* Jeekel, 1984, *L. alisonae* Jeekel, 1984, *L. modestus* Chamberlin, 1920 (type species) and *L. perporosus* Jeekel, 1984 from Tasmania, *L. martini* (Carl, 1902) from Victoria, and 23 new species: *L. anas*, *L. bashfordi*, *L. clivulus*, *L. cognatus*, *L. cornutus*, *L. devexus*, *L. hamatus*, *L. horridomontis*, *L. inopinatus*, *L. latus*, *L. montanus*, *L. orarius*, *L. peninsulensis* and *L. plomleyi* from Tasmania, and *L. blackwoodensis*, *L. catrionae*, *L. dignomontis*, *L. gippslandicus*, *L. johnsi*, *L. macedonensis*, *L. milledgei*, *L. otwayensis* and *L. tarrabulga* from Victoria. The new genus *Tasmanopeltis*, close to *Lissodesmus*, is erected for *T. grandis* sp. nov. from Tasmania.

### Keywords

Diplopoda, Polydesmida, Dalodesmidae, millipede, Australia, Tasmania, Victoria, spiracles, sphaerotrichomes

### Introduction

Tasmania and Victoria are home to a diverse group of dalodesmid Polydesmida with well-developed paranota, a long dorsal seta near the posterior corner of each paranotum (Fig. 1) and fairly uniform gonopod structure. Currently all such forms are referable to either *Lissodesmus* Chamberlin, 1920 or *Dasystigma* Mesibov, 2003. In this paper I place 14 new Tasmanian and nine new Victorian species in *Lissodesmus*. The expanded genus is far from homogeneous, but it is not yet clear how it should be divided into monophyletic subgroups. An unusual form from north-eastern Tasmania is placed in *Tasmanopeltis* gen. nov., close to *Lissodesmus*.

**Characters.** Tasmanian and Victorian dalodesmids with a head + 20 segments, well-developed paranota and a long posterior corner seta (Fig. 1) are here called the “*Lissodesmus* group”. All species have four main branches or processes on the gonopod telopodite arranged as shown in Fig. 2. In naming these processes I follow Jeekel (1983, 1984), but Jeekel’s “solenomerite” is here “solenomere”. This is the mesal or anteromesal process in which the prostatic groove terminates. In *L. martini* (Carl, 1902) it was called the “principal branch” (*Hauptast*) by Carl (1902) and the “seminal groove branch” (*Samenrinnenast*) by Attems (1940), while Chamberlin (1920) called it the dorsal branch of the mesal spur in *L. modestus* Chamberlin, 1920.

The telopodite continues distally from the solenomere origin as the prefemoral process (**pf**) (Carl: “neighbouring branch” (*Nebenast*); Attems: “tibiotarsal branch” (*Tibiotarsalast*)). Arising on the lateral or anterolateral side of the prefemoral process is the femoral process (**f**) (Carl: “secondary branch” (*sekundärer Ast*) of the “neighbouring branch”; Attems: “short side branch” (*kurzer Seitenast*)). Finally, arising posterior to the solenomere is the tibiotarsus (**tt**) (Chamberlin: ventral branch of the mesal spur; Attems: “spine” (*Dorn*)).

The process names as used here are only conventional labels. Because the development of the telopodite in male Polydesmida is so abrupt and so cryptic, it is not certain that the processes are homologous with the podomeres suggested by the process names, i.e. prefemur, femur, tibia and tarsus.

In addition to the main telopodite processes, most species in the *Lissodesmus* group have at least one mesolaterally flattened projection on the posterior surface of the prefemoral process. In accord with Jeekel (1984) this projection is here called an “uncus” (**u** in Fig. 2), although it is not always hook-shaped.

As background to a discussion of classification in the *Lissodesmus* group, I review here a number of characters, beginning with the telopodite processes. Apart from *L. adrianae* Jeekel, 1984, *L. alisonae* Jeekel, 1982, *L. martini* (Carl, 1902), *L. modestus* Chamberlin, 1920 and *L. perporosus* Jeekel, 1984, all *Lissodesmus* species mentioned in this section are new species described below.

**Solenomere.** The solenomere is the least variable of the telopodite processes. It typically arises at one-third to half the length of the telopodite on the anteromesal surface, bending posteriorly and often lying at the bend on a broad indentation in the telopodite body. The prostatic groove typically enters the solenomere on its anterior side near its base, then abruptly curves to run on the posteromesal side, terminating at the solenomere's fine, generally truncated tip. The solenomere varies very little in size relative to the telopodite as a whole from species to species. In most species the solenomere is directed distally or posterodistally, but in *L. devexus* (Fig. 32) it points posteriorly. A small structure like a toothed half-collar is found in some species on the anterior or anteromesal side of the solenomere close to its tip (e.g. in *L. martini*, Fig. 50). This structure is reduced to a small, pointed projection in some species (e.g. *L. modestus*, Fig. 53) and is absent in *L. adrianae*, *L. devexus*, *L. horridomontis*, *L. peninsulensis*, *T. grandis* and all four *Dasytigma* species (Mesibov, 2003b). The most unusual solenomeres are found in *L. peninsulensis*, in which the solenomere curves helically (Fig. 60), and in *L. tarabulga*, which in place of a subapical projection has a large, stout process arising about midway along the solenomere on its anterior side (Fig. 66).

**Prefemoral process.** The tip of the prefemoral process generally bends posteriorly. The amount of bending varies from a slight curvature in *L. peninsulensis* (Fig. 61) to a 180° turn in *L. catrionae* (Fig. 22). In *L. adrianae* (Fig. 12) and *L. modestus* (Fig. 53), the tip is erect. In *L. dignomontis* (Fig. 35) and *L. johnsi* (Fig. 45) the tip is completely unarmed but in other species it bears teeth or tooth-like projections in a wide range of sizes, shapes, positions and orientations, and the process in many species ends in an elaborate comb (e.g. in *L. macedonensis*, Fig. 48). In most species the tip of the prefemoral process is undivided. The tip is broadly divided in *L. orarius* (Fig. 57) and forked in *L. bashfordi* (Fig. 17). In *L. hamatus* (Fig. 39), *L. horridomontis* (Fig. 41), *L. inopinatus* (Fig. 43) and *L. otwayensis* (Fig. 59) the distal portion of the process is abruptly shifted laterally, with a low "shoulder" projection marking the mesal end of the bend. In *T. grandis* (Fig. 68) this "shoulder" is larger and projects distally as a separate sub-process. The prefemoral process varies in length and armature in *L. devexus* (Figs 32, 33), but in other species these two features are more stable.

**Femoral process.** The most complex femoral processes are found in *Dasytigma* species, in which the process is variously divided near its tip and armed (Mesibov, 2003b). In other species the process is typically a smooth, bluntly pointed bar or blade, often with a posterior branch (e.g. in *L. alisonae*, Fig. 14). In *T. grandis* (Fig. 68) the tip of the femoral process is expanded and carries a few blunt projections. *Lissodesmus* group species also vary in where the femoral process originates on the telopodite, i.e. proximal or distal to the solenomere origin. In four species the femoral process extends distally as far as the tip of the prefemoral process: *L. bashfordi* (Fig. 18), *L. dignomontis* (Fig. 35), *L. johnsi* (Fig. 45) and *L. modestus* (Fig. 52). Whether the femoral process in these species has become a functional adjunct of the prefemoral process is unknown.

**Tibiotarsus.** In most species the tibiotarsus is a simple rod directed posterodistally, but in *L. devexus* the process is directed posterobasally (Fig. 32). The tibiotarsus originates just posterior to the solenomere in all but the four *Dasytigma* species, in which the origin is much further lateral, roughly halfway around the telopodite body towards the origin of the femoral process. The tip of the tibiotarsus is expanded and turned distally in a number of species, and in *L. catrionae* (Fig. 22), *L. cornutus* (Fig. 30), *L. horridomontis* (Fig. 41) and *L. montanus* (Fig. 55) the tip is armed with blunt, tooth-like, marginal projections. A curious feature of the tibiotarsus in *L. devexus* is a series of annular "wrinkles" visible at high magnification (Fig. 31). The "wrinkles" give the impression that the tibiotarsus has been compressed along its long axis before the cuticle had thoroughly hardened. In *L. johnsi* (Figs 44, 45) the tibiotarsus is fan-shaped and marginally toothed.

**Uncus.** Many species have a single small uncus similar to the one shown schematically in Fig. 2, and some have several mesolaterally flattened projections in the same region, i.e. between the solenomere origin and the tip of the prefemoral process. Because these processes vary in shape, number and position, it is not clear whether they should be considered homologous, e.g. whether either or both of the small, ridgelike projections in *L. perporosus* (Figs 62, 63), partway along the prefemoral process on its posterior surface, are developmentally equivalent to the large, arcuate structure in *L. peninsulensis* (Fig. 61). Assuming homology, the most variable and unusual uncus is found in *L. devexus* (Figs 32, 33). In specimens from the type locality the uncus is a long, blade-like structure parallel to the tip of the prefemoral process, while in specimens from a nearby locality the uncus is merely a low ridge with a slightly hook-shaped tip.

**Telopodite setae.** All species have sparse, long setae on the posterior surface of the proximal portion of the telopodite. The most distal setae are typically at the level of the solenomere origin or just beyond. In *L. otwayensis* a row of large setae continues distally almost to the level of the uncus (Fig. 58), and in *L. adrianae* the most distal setae are close to the apex of the prefemoral process (Fig. 11).

**Body size.** Overall length ranges from c. 11 to c. 35 mm, but length measurements of preserved specimens are affected by the degree to which each prozonite is telescoped into the next metazonite headwards. The size measure used here, *H*, is the height of segment 12 as viewed from the rear (see Fig. 3), i.e. in the plane of the posterior edge of the metazonite. *H* was measured  $\pm 0.1$  mm on a male of each species judged to be typical; see remarks on individual species for comments on within-species variability. Between species *H* varies from 1.2 to 3.3 mm.

**Antennomeres.** Chamberlin (1920: 135) observed that the antenna in *L. modestus* had "the second and sixth articles longest, the third a little shorter, the fourth and fifth much shorter". In redescribing *L. modestus* from topotypical material, Jeckel (1984) measured the relative lengths of antennomeres 2 to 6 as 1.00, 0.90, 0.65, 0.65 and 0.85 and commented: "In his description Chamberlin stated that the 2nd and 6th antennomeres are the longest with which present observations do not agree. It seems possible that Chamberlin



actually meant the length of the 2nd and 6th to 8th antennomeres" (p. 94). I have not seen Jeekel's material, but I have examined the *L. modestus* holotype and Chamberlin's description is correct. The difference between the two descriptions is almost certainly due to differences in the degree to which the antennomeres are telescoped in the preserved specimens, and in how antennomere length was measured. Antennomere proportions vary little in the *Lissodesmus* group (Fig. 69; see also Fig. 2 in Mesibov, 2003b), with antennomere 2 slightly longer than or about equal to 6, followed by 3, then by the more or less equal 4 and 5; antennomere 6 is invariably the widest.

**Paranota.** The size, shape and setation of paranota vary from anterior to posterior within individual specimens in the *Lissodesmus* group, as elsewhere in the Polydesmida. Differences can also be seen when comparing the same segment from individual to individual: in the shape of the paranotal margin as viewed from above; in the degree of "inflation" of the paranota in a transverse section of the segment; in the number, position and degree of definition of marginal notches; and in the presence/absence of setae associated with the notches. This variation devalues some paranotal characters for separating species. However, the ratio *R* of paranotal width to prozonite width (Fig. 3) is useful. In the 29 species considered here, *R* of segment 12 ranged from 1.3 ("reduced paranota") to 1.8 ("wide paranota"). Maximum prozonite width is tightly correlated ( $r^2 = 0.96$ ;  $n = 29$ ) with *H* in individual specimens, but *R* is apparently not correlated with *H* between species. A second useful paranotal character is the degree to which the posterior corner is turned up (Figs 4, 28). Turned-up corners are associated with reduced relative width, occurring in all five species with *R* = 1.3, two of the eight species with *R* = 1.4 and two of the 13 species with *R* = 1.5.

**Ozopores.** The pore formula is normal for head + 20 segment Polydesmida, i.e. ozopores on segments 5, 7, 9, 10, 12, 13, 15–19, except for *L. perporosus*, which has the formula 5, 7, 9–19. Ozopores open dorsolaterally near the paranotal margin, more or less close to the posterior corner (Fig. 70).

**Spiracles.** In most *Lissodesmus* species the spiracles are as shown in Fig. 5A for *L. modestus*. They have thick and rounded rims, small apertures, and no projecting structures. On each diplosegment the anterior spiracle opens just above the coxa of the anterior leg, with a thin shelf-like projection of the body wall separating the two. The posterior spiracle opens about midway between the anterior and posterior legs. In both sexes in *Dasystigma* species and in *Tasmanopeltis grandis* (Fig. 5B) the spiracle rims are very thin and the aperture relatively wide, and a dense mass of hair-like structures projects from the opening. Further, the posterior spiracle lies immediately adjacent to the anterior spiracle in *T. grandis* and in *D. bonhami* Mesibov, 2003 (Mesibov, 2003b, Fig. 5A) and *D. margaretae* Mesibov, 2003 (Mesibov, 2003b, Fig. 5C, D). Stadium 5 *T. grandis* have spiracles of normal appearance and at normal spacing; the spiracles become progressively "hairier" and closer together in stadia 6, 7 and 8. In both sexes of *L. anas* (Fig. 5C), a dense mass of hair-like structures obscures the spiracle openings. The size, shape and position of the *L. anas* spiracles are seen in cleared preparations to be the same as in *L. modestus*. A small clump of hair-like structures arises from

the body wall just posterior and ventral to the posterior spiracle (just visible in Fig. 5C). Just anterior and ventral to the anterior spiracle, a long, rigid "fox tail" of hair-like structures arises and extends posteriorly almost to the posterior spiracle. Many of the hair-like structures associated with both spiracles are forked near their base. The "fox tail" structure has not, to my knowledge, been noted elsewhere in the Diplopoda. I have not seen stadium 6 or younger *L. anas*, but a less well-developed anterior "fox tail" and posterior clump are present in stadium 7.

**Limbus.** Under relatively low magnification (200 $\times$ ), the limbus appears to be composed of simple, straight elements. Under higher magnification the elements in *L. latus* are seen to be strongly tapering structures (Fig. 6A), while in *L. hamatus* each tapering element has a row of sharp, posteromesally directed teeth on the mesal surface (Fig. 6B). The limbus in other species has not been examined at high magnification.

**Epiproct.** In most *Lissodesmus* group species the epiproct ends in two short, well-separated, rounded bumps (Fig. 7A). The projections are longer in some *Lissodesmus* species (Fig. 7B), giving the epiproct a forked appearance even at low magnification.

**Podomeres.** As usual for Polydesmida, legs close to the gonopods in *Lissodesmus* group males are greatly swollen compared to the corresponding legs in females. The prefemur has a rounded dorsal projection, and some dorsal expansion is usually also seen on the femur (Fig. 71). Species differ in the degree of swelling, e.g. *L. anas* (Fig. 71ana) has slender legs and *L. macedonensis* (Fig. 71mac) has thick, robust ones. In some species the tarsus is shorter than the femur (e.g. *L. horridomontis*, Fig. 71hor), in others the same length (e.g. *L. perporosus*, Fig. 71per), and in still others distinctly longer (e.g. *L. peninsulensis*, Fig. 71pen). Tibiae are also variable, with a ventral, distal swelling apparent in some species (e.g. *L. modestus*, Fig. 71mod).

**Sphaerotrichomes.** I presented some preliminary observations on male leg setae (Mesibov, 2004a) and reported that beginning with leg 3, most legs in male *L. modestus* have sphaerotrichomes on the prefemur, femur, postfemur, tibia and tarsus. An erratum noted that sphaerotrichomes were present only on the tibia and tarsus in *L. modestus*. However, my original observations were correct (Fig. 8A), and sphaerotrichomes can, in fact, be seen on the *L. modestus* femur in Fig. 2G of Mesibov (2004a). The same error was made by Jeekel (1984) in his redescription of *L. modestus* ("globular setae on tibia and tarsus", p. 93), and by Johns (1964) in his revision of *Pseudopronopeltis*, including what is now *L. martini*. In my own case the error arose because I habitually viewed legs from the side, and in this orientation the dense "brush" setae on the proximal podomeres can hide sphaerotrichomes lying mainly on the midventral line. The true distribution of sphaerotrichomes can be revealed using scanning electron microscopy, or by clearing the leg (e.g., with 60% lactic acid) and viewing it from beneath with a light microscope and substage illumination. Sphaerotrichome numbers and distributions vary from leg to leg (Mesibov, 2004a). For the present study I cleared and examined leg 6 from one male of each of the 29 species under consideration. Sphaerotrichomes were found on the prefemur, femur, postfemur, tibia and tarsus of 24 species, but in some

cases "presence" on the prefemur amounted to only one or two sphaerotrichomes. Sphaerotrichomes were seen on the tarsus and tibia only in *L. devexus* and *L. milledgei*; on the tarsus, tibia and postfemur in *L. cornutus* and *L. horridomontis*; and on the tarsus, tibia, postfemur and femur in *L. orarius* (Fig. 8B). Absence of sphaerotrichomes from podomeres was clearly correlated with a lower total number of sphaerotrichomes on the leg, indicating that absence from some leg 6 podomeres in the five named species results from variation in a quantitative character. A similar quantitative variation is seen in individual specimens: the total number of sphaerotrichomes per leg decreases from leg 3 rearwards, and the last legs typically have sphaerotrichomes on tibia and tarsus only. In most *Lissodesmus* species the sphaerotrichome shafts are gradually tapered, as shown for *L. modestus* in Fig. 2D in Mesibov (2004a), but in some species, e.g. *L. martini*, the tips of the shafts are slightly expanded, as in *Bromodesmus* species (Fig. 2B in Mesibov, 2004a).

**"Furriness".** The new species *L. cognatus* and *L. latus*, are "furry" in portions of their respective ranges. The "fur" (Fig. 9B) consists of long, thin setae sparsely distributed on the collum and metatergites of all males and females collected in these areas (for locations, see remarks on the respective species). Furry individuals have the usual complement of longer setae on the head, the anterior portion of the collum and the posterior portion of the preanal segment. Differences between the gonopods of furry and typical forms are minor. The functions of the fur are unknown; furry specimens are found in the same microhabitats as non-furry forms.

**Juvenile stadia.** The typical pattern of paranotal development in the *Lissodesmus* group is shown in Fig. 10 for *L. perporosus*. Stadium 5 and younger individuals have prominent teeth armed with setae on the lateral and posterior margins. As the individual matures, the lateral teeth are progressively reduced to marginal sections delimited by small notches. All or most of the lateral setae are lost; the most anterior of the lateral setae is the one most frequently retained (Fig. 70). The posterior marginal teeth disappear in most species but are retained in stadium 8 of Tasmanian *L. latus* and Victorian *L. blackwoodensis*, *L. dignomontis*, *L. gippslandicus*, *L. johnsi*, *L. macedonensis*, *L. martini* and *L. tarrabulga* (Fig. 70). The lateral margin of the paranotum is typically straight and parallel to the longitudinal body axis in early stadia, curving as the individual matures (Fig. 10).

## Classification

Jeckel (1984) reviewed the six species then known in the *Lissodesmus* group: *L. adrianae*, *L. alisonae*, *L. margaretae*, *L. martini*, *L. modestus* and *L. perporosus*. The gonopod structure generalised in Fig. 2 clearly set these six species apart from the other dalodesmids with a head + 20 segments known at the time from Tasmania and Victoria, namely *Gasterogramma psi* Jeckel, 1982, *Gephyrodesmus cineraceus* Jeckel, 1983 and *Tasmanodesmus hardyi*. Jeckel (1984) applied to that concept the oldest available name, *Lissodesmus*.

There are now 33 species in the group, and some subgrouping is apparent. It is less clear how to translate that structure

into genera (or subgenera, which in myriapodological practice are often "holding bays" for future genera). There are few useful non-sexual characters, and gonopod character states seem to be almost randomly mixed through the group. I have therefore looked for discontinuities: multi-character morphological gaps between species.

Four species of *Dasystigma* were distinguished by an unusually wide separation between solenomere and tibiotarsus, by the presence of hair-like structures in the spiracles, and by a close similarity in body size and colour, overall gonopod structure and paranotal form (Mesibov, 2003b). Here a new genus is erected for *Tasmanopeltis grandis*, remarkable for its exceptionally large size, spiracles with hair-like structures, process origins unusually far distal along the telopodite, and a unique, large, distal projection on the prefemoral process.

The other species in the *Lissodesmus* group include many which look to be closely related (i.e., have similar gonopods) and occur in the same region, e.g. *L. dignomontis*, *L. johnsi* and *L. tarrabulga* in Gippsland, and *L. bashfordi* and *L. modestus* in south-east Tasmania. However, I here leave *Lissodesmus* as a heterogeneous assemblage of 28 species. It thus joins *Icosidesmus* in New Zealand (Johns, 1964) and *Gnomeskelus* in southern Africa (Lawrence, 1953, 1958) as an unresolved knot of relationships in Dalodesmidae. If Shelley (1990a) is correct, it adds to a long list of large, "difficult" genera in many other millipede families. *Lissodesmus* may not be the largest such group in the south-east Australian Polydesmida; *Tasmaniosoma* Verhoeff, 1936 contains a similarly puzzling diversity of forms (Mesibov, in preparation).

## Ecology and life history

In Tasmania, species in the *Lissodesmus* group are found in moist leaf litter, in and under rotting wood, under stones, in the upper layers of richly organic soil and in the moist skirt of rotted bark, twigs and leaves around the base of larger trees. They occur in cool temperate rainforest, wet eucalypt forest, dry eucalypt forest and subalpine woodland. They are particularly abundant in forest growing on fertile soils (e.g., those derived from Tertiary basalt). Within the Tasmanian annual rainfall range of c. 550–3500 mm they appear to be most abundant at intermediate values, c. 1000–2000 mm. *Lissodesmus* group species are occasionally found in alpine areas, grassy woodland and coastal scrub, but are only rarely seen in moorland, heathland and grassland. A few species are accidental cave inhabitants. No species have yet been found in long-established gardens of exotic plants, but *L. alisonae* and *L. perporosus* can be abundant in plantations of *Pinus radiata* (Bonham et al., 2002; Mesibov, 2005).

Victorian *Lissodesmus* species are so far known from cool temperate rainforest, wet eucalypt forest and dry eucalypt forest in areas with an annual rainfall greater than c. 800 mm. They are mainly found in well-rotted eucalypt logs and in accumulations of moist peaty material in surface depressions on such logs. In my own, limited experience, Victorian *Lissodesmus* are very rarely seen away from logs at lower elevations, but are sometimes found in leaf litter in the high country (>900 m).

Species in the *Lissodesmus* group are typically found sheltering in mixed-age aggregations. In Tasmania, life histories of *Dasystigma*, *Lissodesmus* and *Tasmanopeltis* appear to be only weakly seasonal. Throughout the year, a collector can find adults (including pairs in *copula*) and most juvenile stadia, even in subalpine habitats. Victoria has hotter and drier summers than Tasmania, and Victorian *Lissodesmus* may be more seasonal than their Tasmanian congeners.

All species in the *Lissodesmus* group are cryptic in their habits, but some Tasmanian species, notably *L. perporosus*, can be found wandering at night. Judging from gut contents, *Lissodesmus* group species feed on well-rotted wood and richly organic soil particles. Nothing is known of their parasites or predators, but small mites (unidentified) are often found on older individuals of both sexes.

### Biogeography

Mesibov (2003b) reported that *Dasystigma* in Tasmania formed a mosaic complex of the kind first clearly described by Shelley (1990a, 1990b). The biogeographical situation is more complicated in Tasmanian *Lissodesmus*. While mosaics can sometimes be found (e.g. in the north-east with *L. adrianae*, *L. alisonae* and *L. hamatus*; see Mesibov, 1997), in most parts of the island species are sympatric. Three *Lissodesmus* species are commonly found at a single site. Four species (*L. anas*, *L. clivulus*, *L. latus* and *L. perporosus*) have been collected in forest adjoining Balfour in the north-west, and five *Lissodesmus* species can occur in the same patch of forest in parapatric overlap zones, such as the Weavers Creek parapatric zone in the north-east (Mesibov, 1997; *L. adrianae*, *L. alisonae*, *L. cognatus*, *L. devexus* and *L. hamatus*), which is also home to *Tasmanodesmus hardyi* and *Tasmanopeltis grandis*. Two species, *L. cognatus* and *L. devexus*, seem to have naturally disjunct areas of occurrence.

In Victoria, *Lissodesmus* distributions are mainly allopatric, but *L. blackwoodensis* and *L. macedonensis* have been found together near Blakeville, *L. gippslandicus* and *L. dignomontis* near Allambee, *L. gippslandicus* and *L. johnsi* near Yarragon, and *L. gippslandicus* and *L. tarabulga* near Balook. *L. martini* and *L. milledgei* probably co-occur near the Acheron Gap in the Yarra Ranges and at The Beeches near Marysville. Collections to date in Gippsland indicate that *L. dignomontis* and *L. johnsi* are parapatric south-west of Trafalgar, and that *L. gippslandicus* and *L. martini* are parapatric near the Narracan Creek valley.

*Lissodesmus* has so far been sampled at only c. 60 sites in Victoria, compared to c. 1200 sites in Tasmania for *Dasystigma*, *Lissodesmus* and *Tasmanopeltis*, but the area over which *Lissodesmus* could be expected to occur in Victoria is substantial. Including only the higher-rainfall, southern portions of the Western and Eastern Uplands, and both of the Southern Uplands blocks, I estimate this area to be 80 000 km<sup>2</sup>, which is larger than Tasmania. Although much of the pre-European cover of wet forest has been lost from this area, it is likely that new species of *Lissodesmus* remain to be found in the Grampians, East Gippsland and physiographically isolated portions of the eastern highlands.

New, narrow-range species of Tasmanian *Lissodesmus* are also likely to be recognised in future, as there are female (and a few aberrant male) specimens in collections which I cannot confidently assign to any of the species described below. Several of these come from Flinders Island, which has not yet been surveyed carefully for millipedes.

### Conservation

The Tasmanian species *L. clivulus*, *L. cognatus*, *L. horridomontis*, *L. orarius* and *L. peninsulensis* have extents of occurrence (range envelopes) of 300 km<sup>2</sup> or less. Nevertheless, local populations of these species are often large and well-distributed through extensive patches of native vegetation which are unlikely to be cleared in the foreseeable future. *L. montanus*, *L. peninsulensis* and *L. plomleyi* have larger ranges but seem to be naturally rare. None of these three species appears to be under threat. The range of *L. montanus* includes parts of several large, formal reserves. *L. peninsulensis* and *L. plomleyi* are both known mainly from areas of public land within which there are sizeable informal reserves of riparian forest, old-growth eucalypt forest, and steep and rocky ground. My field experience over the past 25 years is that Tasmanian *Lissodesmus* species tolerate the clearfelling, burning and regeneration of wet eucalypt forest habitat (Taylor, 1990; Mesibov, unpublished results).

Field studies aimed at establishing range boundaries and habitat preferences have so far been carried out for two Tasmanian *Lissodesmus* species. Originally thought to be rare (Mesibov, 1992), *L. orarius* was later found to be the dominant *Lissodesmus* species in coastal habitats between the Pedder and Pieman Rivers on the west coast (Mesibov, unpublished report to the Tasmanian Conservation Trust, 1993). Distribution mapping of *L. alisonae* increased the number of known localities from nine to 93, and the range envelope (minimum convex polygon) from 1551 to 4965 km<sup>2</sup> (Mesibov et al., 2002). Within its range, centred on the densely settled Tamar Valley, *L. alisonae* occurs in all native forest types as well as in native/exotic vegetation mixtures in city parks, and has recently been found to be abundant in a second-rotation *Pinus radiata* plantation (Mesibov, 2005).

Tasmania is a largely forested island, and about 40% of that forest is currently in formal reserves. The distribution of those reserves is the result, in part, of efforts to secure large, regionally representative blocks of little-disturbed native forest communities. The situation in Victoria is very different. Much of the wet native forest present when Europeans arrived in the 19th century has been cleared for agriculture or forestry plantations, and much of the surviving forest, reserved or not, has been degraded by frequent burning and weed invasion. In my field experience in Victoria, populations of *Lissodesmus* species other than *L. gippslandicus*, *L. martini* and *L. otwayensis* seem to be small and restricted to little-disturbed native forest remnants.

*L. johnsi* was first collected in 1890 near Trafalgar in the Latrobe Valley, probably in the area's tall, dense eucalypt forests (Adams, 1978). The area is now almost entirely covered with pasture and forestry plantations. Recent searches for

*L. johnsi* have so far yielded specimens from forest remnants at only two localities, both near Trafalgar and about 5 km apart.

## Methods

Specimens were usually killed and preserved in 70–80% ethanol. For some species, vouchers preserved for molecular analysis in 95% ethanol have been deposited in QVM. Preliminary drawings on graph paper were made using an eyepiece grid; the grid was calibrated for measurements of body parts. Gonopods and male sixth legs were cleared and temporarily mounted in 60% lactic acid; other body parts were temporarily mounted in a glycerine-water mixture. A Philips Electroscan ESEM 2020 operated in high-vacuum mode was used to examine material which had been air-dried before sputter-coating with gold. SEM images were acquired digitally.

This review is based on more than 2000 museum samples containing more than 6500 specimens. Details of specimens other than holotypes and paratypes have been omitted from the "Material Examined" sections and are given in a separate document ("*Lissodesmus* supplement") available on the *Memoirs of Museum Victoria* website, or from the author, or from the Curator of Zoology at the Queen Victoria Museum and Art Gallery.

In the text, Tasmanian localities are given with a UTM grid reference (Grid Zone Designation 55G) and the (calculated) equivalent latitude/longitude, in both cases with respect to the AGD66 datum. Victorian localities are given with latitude/longitude with respect to the WGS84 datum.

Abbreviations are as follows: AM, Australian Museum, Sydney, NSW; MCZ, Museum of Comparative Zoology, Cambridge, Mass., USA; NMV, Museum Victoria, Melbourne, Vic.; QVM, Queen Victoria Museum and Art Gallery, Launceston, Tas.; TM, Tasmanian Museum and Art Gallery, Hobart, Tas.; WAM, Western Australian Museum, Perth, WA.

## Taxonomy

In the case of millipedes distinguished primarily by gonopod differences, keys and species diagnoses are necessarily verbose and often very hard to understand, even for a specialist. The most taxonomically useful part of a millipede species description is the gonopod illustration, and readers are encouraged to look first at the scanning electron micrographs and line illustrations provided.

Note that in the telopodite descriptions and drawings a "mesal" view is one centred on the solenomere, "lateral" on the femoral process, "anterior" on a line roughly midway between the origins of these two processes on the anterior surface, and "posterior" on a line roughly 180° around the telopodite from "anterior". This convention has been adopted for convenience; as seen in the SEM views, the in situ orientation of the telopodite varies considerably from species to species.

The five species *L. adrianae*, *L. alisonae*, *L. martini*, *L. modestus* and *L. perporosus* have already been carefully described by Jeekel (1983, 1984); brief, partial redescriptions and new illustrations are included here only for the sake of consistency.

Order **Polydesmida** Leach, 1815

Suborder **Dalodesmidea** Hoffman, 1980

**Dalodesmidae** Cook, 1896

***Lissodesmus*** Chamberlin, 1920

*Lissodesmus* Chamberlin, 1920: 135.—Attems, 1940: 490.—Jeekel, 1970: 336.—Jeekel, 1983: 150.—Jeekel, 1984: 89.—Mesibov, 2003b: 198.

*Pseudoprionopeltis* (*Australopeltis*) Johns, 1964: 47.

*Australopeltis* Hoffman, 1980: 184.—Shelley et al., 2000: 86.

*Type species.* *Lissodesmus modestus* Chamberlin, 1920, by original designation.

*Diagnosis.* Small to medium-sized dalodesmids (11–23 mm long, 1.2–2.2 mm vertical diameter) with head + 20 segments, normal pore formula (except *L. perporosus*), well-developed paranota with long posterior corner seta, spiracles well-separated on diplosegments and without emergent hair-like structures. Telopodite with small mesal or anteromesal solenomere and tibiotarsus, small to large lateral or antero-lateral femoral process and large central prefemoral process; solenomere arising at one-third to one-half the telopodite height. Prefemoral process tip typically undivided; in *L. orarius* divided apically into two posteriorly directed branches.

*Remarks.* Chamberlin (1920) erected the monotypic genera *Lissodesmus* and *Tasmanodesmus* for the Tasmanian species *L. modestus* and *T. hardyi*. The two genera were ignored by Verhoeff (1932, 1936) on the grounds that Chamberlin had published no illustrations, and were regarded as genera of uncertain family placement by Attems (1940). Chamberlin believed the two genera were closely related, but as shown in a recent redescription (Mesibov, 2004b) *T. hardyi* is substantially different in gonopod structure from all other Tasmanian dalodesmids, and the posterior corner seta in *T. hardyi* is short and inconspicuous.

*Pseudoprionopeltis martini* Carl, 1902 from Melbourne was included by Johns (1964) in his revision of New Zealand *Pseudoprionopeltis*. He erected the subgenus *Australopeltis* for *P. martini* and illustrated the anterior segments and gonopod of a specimen from Cockatoo Creek in the Museum Victoria collection. One of the characters used by Johns to diagnose the new subgenus was the posterior corner seta, which he described as "a long seta inserted just anterior and dorsal of the [posterior paranotal] tooth" (Johns, 1964: 47).

In his reclassification of the Diplopoda, Hoffman (1980) raised *Australopeltis* to a genus. Although Chamberlin (1920) had provided a verbal description of the *L. modestus* gonopod, Hoffman (1980: 150) regarded the gonopod structure of *Lissodesmus* as "still unknown". Nevertheless, he placed both *Australopeltis* and *Lissodesmus* in Dalodesmidae Cook, 1896. In doing so, Hoffman formalised the observation by Brolemann (1916) that the circular gonopod aperture in *P. martini* indicated an affinity between that species and Semnosomidae Brolemann, 1916, which Hoffman (1980) considered a synonym of Dalodesmidae.

Jeekel (1983) made *Australopeltis* a synonym of *Lissodesmus* after examining fresh material of Victorian *L. martini* and Tasmanian *L. modestus*. Both species had been collected by Jeekel during a 1980 field trip to Australia. Jeekel did not redefine *Lissodesmus* in the 1983 paper, instead referring the reader to "a previous paper", then in press, which actually appeared the following year (see below). However, Jeekel (1983) gave a detailed description and clear illustrations of a male of *L. martini* from Ferntree Gully National Park.

In 1984, Jeekel redescribed *L. modestus* from topotypical material and added four new Tasmanian species to the genus: *L. adrianae*, *L. alisonae*, *L. margaretae* and *L. perporosus*. In his key to the genera of Tasmanian Polydesmida, he noted that *Lissodesmus* could be separated from *Tasmanodesmus* by the presence in the former of "a long hair mesad of caudal edge of paranota" (Jeekel, 1984: 89), i.e. the posterior corner seta. *L. margaretae* Jeekel, 1984 was recently removed from *Lissodesmus* and placed with three new Tasmanian species in the new genus *Dasystigma* (Mesibov, 2003b).

As delimited here, *Lissodesmus* is what remains of the group of south-eastern Australian dalodesmids with a head + 20 segments and a long posterior corner seta after exclusion of *Dasystigma* (spiracles with hair-like structures, wide separation between solenomere and tibiotarsus origins, complex femoral process) and *Tasmanopeltis* gen. nov. (spiracles with hair-like structures, relatively long unbranched portion of telopodite, mesal "shoulder" process on prefemoral process). *Lissodesmus* is thus a product of "taxonomic erosion" of a group of similar taxa and is not defined by a set of unique character states. However, it is readily distinguished from the other regional H+20 dalodesmids *Atalopharetra* Mesibov, 2005, *Bromodesmus* Mesibov, 2004, *Gasterogramma*, *Gephyrodesmus*, *Tasmanodesmus* and *Victoriombrus* Mesibov, 2004 by its possession of a long seta at the posterior corner of each paranotum and by the gonopod structure shown schematically in Fig. 2.

To avoid repetition in the species descriptions below, I have omitted mention of the nearly constant non-sexual features which can be seen in the detailed accounts given by Jeekel (1983; 1984) of *L. adrianae*, *L. alisonae*, *L. martini*, *L. modestus* and *L. perporosus*. Note that the male antennae are separated by about twice a socket diameter unless otherwise specified.

**Distribution.** Throughout Tasmania, and in parts of Victoria with annual rainfall over c. 800 mm.

#### *Lissodesmus adrianae* Jeekel, 1984

Figures 7B, 11, 12, 69adr, 70adr, 71adr, 72 (map)

*Lissodesmus adrianae* Jeekel, 1984: 94.

**Material examined.** Holotype (not seen). Male, Australia, Tasmania. Ben Lomond National Park, 35 km ENE of Evandale, along the road to the top of Ben Lomond, near the park ranger office (approx. EQ530040, 41°30'49"S 147°38'06"E), 23.xi.1980, C.A.W. Jeekel & A. Jeekel-Rijvers. The type is said to be deposited in TM (Jeekel, 1984: 86), but has not yet been received there.

Paratypes. 9 males, 19 females, 10 stadium 7 males, 9 stadium 7 females, 2 stadium 6 females, details as for holotype; female, 10 km NE of Blessington, 23.xi.1980, C.A.W. Jeekel & A. Jeekel-Rijvers.

These specimens are listed as paratypes by Jeekel (1984: 94) but their present locations are unknown and they have not been examined.

Other material. 456 males, 449 females and 357 juveniles from 174 localities (see "*Lissodesmus* supplement" for details).

**Description.** Male c. 18 mm long,  $H = 1.7$  mm. In alcohol, well-coloured specimens under low magnification with light brown body colour dorsally, a transverse band of darker brown near posterior metatergal margins and a small darker brown patch medially, paranota near-white. Antenna moderately long (Fig. 69adr). Paranota fairly wide,  $R = 1.5$  (Fig. 70adr); posterior corners not turned up. Legs robust, tarsus slightly shorter than femur (Fig. 71adr). Epiproct with prominent paired, bluntly rounded projections (Fig. 7B). **Telopodite (Figs 11, 12) sparsely setose almost to apex**, reaching almost to leg 5 when retracted. Solenomere arising at just under half the telopodite height, directed at c. 45° to telopodite axis basally but smoothly curving distally, terminating at one-third to half the prefemoral process length without subapical projection. Tibiotarsus arising slightly distal to solenomere origin, rod-like, bluntly tipped, one-third as long as solenomere and much narrower, directed at c. 45° to telopodite axis. Femoral process arising at level of solenomere origin, straight, blade-like, bluntly pointed, pressed close to prefemoral process, paralleling and reaching halfway to tip of latter, just past apex of solenomere, with a short, bluntly pointed posterior branch at one-third its length. **Prefemoral process about two-thirds the width of telopodite base at origin, straight, mesal edge with a short series of small teeth midway to apex, the latter finely-toothed, anteriorly concave.** No uncus.

**Distribution and habitat.** In wet eucalypt forest, cool temperate rainforest, subalpine woodland and wetter microhabitats in dry eucalypt forest over c. 3500 km<sup>2</sup> in north-east Tasmania (Fig. 72), from 60 m to at least 1050 m. The western and eastern range limits of *L. adrianae* correspond to the biogeographical divides known as the East Tamar Break and Goulds Country Break, respectively (Mesibov, 1994, 1997). The most southerly known occurrence is near Castle Cary, north of Avoca. *L. adrianae* is abundant over most of its range and is by far the commonest dalodesmid in the wetter, forested parts of north-east Tasmania.

**Remarks.** *L. adrianae* varies little in size, coloration and gonopod structure.

#### *Lissodesmus alisonae* Jeekel, 1984

Figures 13, 14, 69ali, 70ali, 71ali, 73 (map)

*Lissodesmus alisonae* Jeekel, 1984: 96.

**Material examined.** Holotype (not seen). Male, Australia, Tasmania. 8 km NW of Frankford, 15 km SW of Beaconsfield, 24.xi.1980, C.A.W. Jeekel & A. Jeekel-Rijvers. The type is said to be deposited in TM (Jeekel, 1984: 86), but has not yet been received there.

Paratypes. 12 males, 21 females, 1 stadium 7 male, 1 stadium 6 female, details as for holotype. These specimens are listed as paratypes by Jeekel (1984: 96) but their present locations are unknown and they have not been examined.

Other material. 286 males, 308 females and 129 juveniles from 181 localities (see "*Lissodesmus* supplement" for details).

**Description.** Male c. 18 mm long,  $H = 1.7$  mm. In alcohol, well-coloured specimens under low magnification with pale brown body colour, pale red posterior metatergal margins. Antenna moderately long (Fig. 69ali). Paranota reduced,  $R = 1.4$  (Fig. 70ali); posterior corners slightly turned up. Legs robust, tarsus about as long as femur (Fig. 71ali). Telopodite (Figs 13, 14) broad at base with abrupt narrowing at start of prefemoral process, reaching almost to leg 5 when retracted. Solenomere arising at about half the telopodite height, directed distally at a small angle to the telopodite axis, terminating with toothed subapical collar at one-third to half the prefemoral process height. Tibiotarsus pointed and mesolaterally flattened, parallel to and almost as wide as solenomere but somewhat shorter and bending slightly laterally. **Femoral process arising just proximal to solenomere origin, not pressed close to prefemoral process, forked at about one-quarter its length, branches more or less equal, blade-like, pointed; anterior branch directed distally and slightly concave posteriorly, terminating just distal to solenomere tip at half to two-thirds the length of prefemoral process, posterior branch gradually curving anteriorly, its tip sometimes lying between anterior branch and prefemoral process. Prefemoral process about half the width of telopodite base, slightly tapered, the tip curved posteriorly with small, blunt, apical and subapical teeth.** Uncus prominent, arising centrally on prefemoral process at just under half the process length (at level of solenomere tip).

**Distribution and habitat.** Common in dry eucalypt forest, wet eucalypt forest and subalpine woodland over c. 6000 km<sup>2</sup> in north central Tasmania (Fig. 73), from sea level to at least 1000 m. The principal eastern range limit for *L. alisonae* is the biogeographical divide known as the East Tamar Break (Mesibov, 1994, 1997), although the species extends eastward along the north coast into the lower Brid River catchment, and a possibly isolated population has been sampled at Cuckoo, near Scottsdale. *L. alisonae* reaches the Don River in the west and Projection Bluff on the north-east corner of the Central Plateau. East of the Plateau *L. alisonae* is parapatric with *L. hamatus* (Mesibov, 1997) along a more or less SW-NE line across the Northern Midlands. *L. alisonae* has been found to be abundant in a second-rotation *Pinus radiata* plantation at Stoodley (Mesibov, 2005) and sometimes occurs in part-native gardens in the Launceston area. Throughout its range, populations are largest in the richly organic soil under dense stands of the understorey tree *Pomaderris apetala*.

**Remarks.** *L. alisonae* varies somewhat in size and coloration, with the smallest and palest forms found in dry forest on relatively infertile soils. In the north-eastern portion of the *L. alisonae* range, the femoral process on the gonopod is longer and the posterior branch less curved (Fig. 14).

#### *Lissodesmus anas* sp. nov.

Figures 4C, 5C, 15, 16, 69ana, 70ana, 71ana, 74 (map)

*Lissodesmus* sp. W1.—Mesibov, 1993: 31.

**Material examined.** Holotype, Male, Australia, Tasmania. Duck Creek, CP408763 (41°44'56"S 145°05'06"E), 160 m, 6.iii.1999, R. Mesibov, QVM 23:45823 (ex QVM 23:40749).

Paratypes. 2 males, north of Pieman Head, CP261860 (41°39'31"S 144°54'41"E), 10 m, 1.vi.1993, R. Mesibov, QVM 23:17656; 2 males, details as for holotype, AM KS91166 (ex QVM 23:40749); 2 males, details as for holotype, QVM 23:40749, dissected; 5 females, details as for holotype, QVM 23:40748.

Other material. 5 males, 9 females and 15 juveniles from Balfour, Heemskirk Road, Mt Frankland, Newdegate Creek, Pieman Head, Piney Creek, Roger River West, Savage River and Wild Wave River (see "*Lissodesmus* supplement" for details).

**Description.** Male c. 16 mm long,  $H = 1.5$  mm. In alcohol, well-coloured specimens under low magnification with pale brown body colour, slightly darker brown near posterior metatergal margins. Antenna long, slender (Fig. 69ana). Paranota reduced with markedly oblique anterior shoulders,  $R = 1.3$  (Fig. 70ana); posterior corners strongly turned up (Fig. 4C), no marginal setae. Legs fairly slender, tarsus about as long as femur, tibia with slight ventral distal swelling (Fig. 71ana). Spiracles apparently typical for genus but with a "foxtail" of hair-like structures arising just anterior and ventral to anterior spiracle, curving dorsally and posteriorly to obscure anterior spiracle and terminating near posterior spiracle; a small clump of hair-like structures arising just posterior and ventral to posterior spiracle (Fig. 5C). Telopodite (Figs 15, 16) more or less uniform in width, slightly curved posteriorly, reaching leg 5 when retracted, with unusually long, sparse setae. Solenomere arising at about half the telopodite height, directed distally before curving slightly posteriorly and laterally at about half its length, terminating with small subapical projection at about half the prefemoral process height. Tibiotarsus more or less cylindrical, about half the solenomere diameter and directed at almost a right angle to telopodite axis, the tip turned distally and pointed with a small, blunt, subapical projection on the anteromesal surface. Femoral process arising proximal to level of solenomere origin, directed distally, closely pressed to prefemoral process, blade-like with a blunt, wide posterior projection at about half the process length, terminating at about half the solenomere length. **Prefemoral process about two-thirds the width of telopodite base at origin, narrowing and bending sharply laterally at about half its length before expanding to very wide, flattened tip curving postero-mesally and aligned parallel to the telopodite axis, terminating in a comb with 20–30 long, posteriorly directed teeth.** Uncus prominent, arising at about half the length of prefemoral process (just proximal to solenomere tip), with a few small, blunt teeth subapically on proximal edge.

**Distribution and habitat.** Known from c. 1300 km<sup>2</sup> in north-west Tasmania, from Roger River West south to Piney Creek (north of Zeehan) (Fig. 74), and from sea level to 450 m. *L. anas* is an uncommon species and is likely to have been overlooked outside its known range. It has mainly been found in wet eucalypt forest and cool temperate rainforest, but two of the paratypes are from partly wooded heathland near the coast at Pieman Head. One specimen was taken from a cave near Savage River.

**Etymology.** Latin *anas* ("duck"), noun in apposition, referring to the type locality, Duck Creek.

*Lissodesmus bashfordi* sp. nov.

Figures 17, 18, 69bas, 70bas, 71bas, 72 (map)

*Lissodesmus* sp. SE1.—Mesibov, 1996: 18.

**Material examined.** Holotype. Male, Australia, Tasmania. Huon River (Manuka Road), DN764287 (43°05'38"S 146°42'36"E), 140 m, 15.v.1997, R. Mesibov, QVM 23:45945 (ex 23:40746).

Paratypes. Male, Dromedary Creek, EN098692 (42°43'46"S 147°07'11"E), 420 m, 19.iii.1992, R. Mesibov, QVM 23:16178; female, same details, QVM 23:16179; male, Bracken Ridge, DN897308 (43°04'31"S 146°52'25"E), 360 m, 17.i.1995, R. Bashford, QVM 23:40745; male, Huon River (Manuka Road), DN764287 (43°05'38"S 146°42'36"E), 140 m, 15.v.1997, R. Mesibov, QVM 23:40746; 7 males, Huon River (Edwards Road), DN792288 (43°05'35"S 146°44'40"E), 100 m, 9.i.2001, R. Mesibov, QVM 23:45946, 2 dissected, in 95% ethanol; male, Huon River (Manuka Road), DN765285 (43°05'45"S 146°42'40"E), 110 m, 3.ii.2001, R. Mesibov, QVM 23:45947, in 95% ethanol; male, Judds Creek, DN976476 (42°55'24"S 146°58'15"E), 390 m, 29.xi.2003, R. Mesibov & K. Bonham, AM KS91167; female, same details, QVM 23:25601; male, same details but DN970463 (42°56'10"S 146°57'49"E), 220 m, QVM 23:25603; male, Peak Rivulet, DN914020 (43°19'59"S 146°53'44"E), 140 m, 12.ix.2005, W. & L. Clarkson, QVM 23:46135.

**Description.** Male c. 15 mm long,  $H = 1.4$  mm. In alcohol, well-coloured specimens under low magnification with very pale brown body colour and red-brown speckling transversely on metatergites, concentrated near posterior margins. Antenna relatively short (Fig. 69bas). Paranota fairly wide,  $R = 1.5$  (Fig. 70bas); posterior corners not turned up. Legs moderately robust, tarsus about as long as femur, tibia with slight ventral distal swelling (Fig. 71bas). Telopodite (Figs 17, 18) reaching leg 5 when retracted. Solenomere arising at one-third the telopodite height, directed posterodistally at about 45° to telopodite axis, curving smoothly laterally and distally, the tip bending abruptly mesally and armed subapically with a small, bluntly pointed projection, terminating at about one-third the prefemoral process height. Tibiotarsus more or less cylindrical, narrower than solenomere, more or less parallel to solenomere but about half its length, curving slightly laterally. **Femoral process arising far distal to solenomere origin at half to two-thirds the telopodite length, slightly flattened near base and curving outwards, distally expanding to a large, leaf-shaped structure bent towards prefemoral process at nearly a right angle and reaching as far distally as that process.** Prefemoral process somewhat more than two-thirds the width of telopodite base, bending sharply posteriorly about midway and curving slightly mesally, terminating in large, flattened, hand-shaped tip with long lateral "thumb" and several short, marginal teeth as "fingers". Uncus small, finger-like, arising just distal to solenomere tip close to mesal edge of prefemoral process.

**Distribution and habitat.** An uncommon species known only from wet eucalypt forest over c. 500 km<sup>2</sup> in south-east Tasmania (Fig. 72), from 100 to 420 m.

**Etymology.** Named for Richard Bashford, who has collected this and many other invertebrate species in his long and productive career in forest entomology in Tasmania.

*Lissodesmus blackwoodensis* sp. nov.

Figures 19, 20, 69bla, 70bla, 71bla, 79 (map)

**Material examined.** Holotype. Male, Australia, Victoria. 3 km NW of Blackwood, 37°27'25"S 144°16'09"E, 560 m, 9.ix.2004, R. Mesibov & T. Moule, NMV K-8933.

Paratypes. 3 males, details as for holotype, AM KS91168; 10 males, details as for holotype, NMV K-8923 to K-8932; 13 females, details as for holotype, NMV K-8934 to K-8946; 13 males, 1 km NE of Blakeville, 37°29'45"S 144°13'07"E, 680 m, 10.ix.2004, R. Mesibov & T. Moule, NMV K-8947 to K-8959; 8 females, same details, NMV K-8960 to K-8967.

**Description.** Male c. 16 mm long,  $H = 1.4$  mm. In alcohol, well-coloured specimens under low magnification with very pale brown body colour, red speckling dorsally on both prozonites and on metatergites, a well-defined transverse band of red speckling near posterior metatergal margins. Antenna moderately long (Fig. 69bla). Paranota reduced but prominent,  $R = 1.4$  (Fig. 70bla); posterior corners not turned up, two inconspicuous posterior marginal teeth on each side. Legs robust, tarsus about as long as femur (Fig. 71bla). Telopodite (Figs 19, 20) with sparse, long, setae extending posterolaterally to just distal of tibiotarsus origin, reaching leg 4 when retracted. Solenomere arising at one-third the telopodite height, directed posterodistally at about 45° to telopodite axis, gradually curving distally, terminating with very small subapical projection at one-quarter to one-third the prefemoral process height. Tibiotarsus more or less parallel to solenomere but shorter, about as wide as solenomere at base and widening distally, forking near tip and terminating in two blunt points. Femoral process arising proximal to solenomere origin, mesolaterally flattened and pressed close at base to prefemoral process, directed distally and widening before terminating in bluntly pointed apex just distal to solenomere tip, anterior to a slightly projecting "shoulder". **Prefemoral process very long, about half as wide as telopodite base, bending laterally just distal to solenomere tip, then bending mesally and curving anterodistally before flexing at nearly 180° to point basally, the lateral edge a comb of c. 40 long, mainly posteriorly directed teeth for nearly its entire length, a few small teeth on mesal edge close to apex.** Uncus small, arising near base of prefemoral process on a ridge formed by the mesal edge of the process.

**Distribution and habitat.** Known from wet eucalypt forest at two localities 6 km apart in the southern portion of Wombat State Forest (Fig. 78).

**Etymology.** Named for Blackwood, the town closest to the type locality, 65 km north-west of Melbourne.

*Lissodesmus catrionae* sp. nov.

Figures 21, 22, 69cat, 70cat, 71cat, 78 (map)

**Material examined.** Holotype. Male, Australia, Victoria. Mt Cole, 37°16'44"S 143°14'23"E, 900 m, 8.ix.2004, R. Mesibov & T. Moule, NMV K-8968.

Paratypes. 3 males, details as for holotype, NMV K-8969 to K-8971, 2 dissected; 7 females, details as for holotype, NMV K-8972 to K-8978; 2 males, Mt Cole, 37°17'09"S 143°14'11"E, 850 m,



8.ix.2004, R. Mesibov & T. Moule, AM KS91169; 3 males, same details, NMV K-8979 to K-8981; female, same details, NMV K-8982.

**Description.** Male c. 16 mm long,  $H = 1.3$  mm. In alcohol, well-coloured specimens under low magnification with very pale brown body colour, sparse red speckling on metatergites, paranota near-white. Antennae moderately long (Fig. 69cat), about  $1.75\times$  a socket diameter apart. Paranota fairly wide,  $R = 1.5$ , anterior shoulders projecting forward (Fig. 70cat); posterior corners not turned up. Legs with high, rounded prefemur (Fig. 71cat), tarsus somewhat longer than femur. Telopodite (Figs 21, 22) with abrupt narrowing at prefemoral process origin, with sparse, long setae extending posterolaterally to just distal of tibiotarsus origin, reaching leg 4 when retracted. Solenomere arising at one-third the telopodite height, directed posterodistally at about  $45^\circ$  to telopodite axis and gradually curving distally, terminating with a small subapical projection at one-third to half the prefemoral process height. Tibiotarsus more or less parallel to solenomere, slightly flattened and wider than solenomere and about as long, bending slightly posteriorly at about half its length, flattening and widening apically with a large, rounded notch opening anteromesally and a small, bluntly pointed projection on anterior (distal) surface at about two-thirds the process length. Femoral process a very narrow, tapering rod arising at about half the telopodite length, directed distally and terminating just distal to solenomere tip. **Prefemoral process arising from lateral half of telopodite base, a little less than half the width of the base, narrow, very long, bending slightly posterodistally at about half its length and flexing  $180^\circ$  at three-quarters its length to terminate in a bluntly pointed apex not far distal to solenomere tip, the posterolateral edge in the distal half of the process a comb of c. 25–30 long, mainly proximally directed teeth.** Uncus large, arising at about one-quarter the length of prefemoral process (just proximal to solenomere tip).

**Distribution and habitat.** Known from wet eucalypt forest on Mt Cole, 50 km north-west of Ballarat (Fig. 78).

**Etymology.** Named for my wife, Catriona (Trina) Moule, in gratitude for her help in the field in Tasmania and Victoria.

#### *Lissodesmus clivulus* sp. nov.

Figures 23, 24, 69cli, 70cli, 71cli, 73 (map)

**Material examined.** Holotype. Male, Australia, Tasmania. The Clump, CQ213361 ( $41^\circ12'23''S$   $144^\circ52'06''E$ ), 190 m, 6.ii.1992, R. Mesibov, QVM 23:45821 (ex QVM 23:17667).

Paratypes. 2 males, details as for holotype, AM KS91170 (ex QVM 23:17667); 11 males, details as for holotype, QVM 23:17667, 3 dissected; 16 females, details as for holotype, QVM 23:17675; male, south of Italian River, CQ180045 ( $41^\circ29'25''S$   $144^\circ49'11''E$ ), 10 m, 30.iv.1993, R. Mesibov, QVM 23:17664.

Other material. 12 males, 26 females and 1 juvenile from Balfour, Brooks Creek, Dawson River, Little Eel Creek, Mt Frankland, Possum Creek, Sardine Creek, Sawards Creek, Sundown Creek, Sundown Point, Temma and The Clump (see "*Lissodesmus* supplement" for details).

**Description.** Male c. 17 mm long,  $H = 1.6$  mm. In alcohol, well-coloured specimens under low magnification with light

brown body colour (unusually, extending to legs and antennae), slightly darker brown transversely on metatergites near posterior margins and distally on antennae. Antenna long, slender (Fig. 69cli). Paranota reduced but prominent,  $R = 1.4$  (Fig. 70cli); posterior corners not turned up. Legs long, slender, tarsus about as long as femur (Fig. 71cli). Telopodite (Figs 23, 24) almost reaching leg 5 when retracted. Solenomere arising at half the telopodite height, directed posteriorly at a large angle (c.  $60^\circ$ ) to telopodite axis, curving slightly laterally, terminating with toothed subapical collar at about one-quarter the prefemoral process height. Tibiotarsus about as wide as solenomere, slightly flattened and tapered near tip, directed posteriorly at almost a right angle to telopodite, curving slightly distally near tip. Femoral process arising at level of solenomere origin, a straight, distally directed blade with a pointed tip, terminating well distal to solenomere tip; at one-quarter to one-third its length with a short, narrow, bluntly tipped branch directed posteriorly and curving distally near its tip. Prefemoral process about half the width of the telopodite base at its origin, expanded past this point, narrowing near apex and bending posteriorly, a few short, large, rounded, proximally directed teeth subapically, the apex flattened and slightly crenulate. Two inconspicuous unci at about half the length of the prefemoral process, not obvious in some specimens.

**Distribution and habitat.** Known from c. 300 km<sup>2</sup> on the west coast of Tasmania (Fig. 73), from just north of the Arthur River to just south of the Italian River, inland to Mt Frankland, and from sea level to 400 m. Despite its small range, *L. clivulus* is sometimes locally abundant. It occurs in wet forest, coastal woodland, tea-tree forest and tea-tree scrub, and (unusually for *Lissodesmus* species) has also been found in low heath (on Mt Frankland, near Balfour).

**Etymology.** Latin *clivulus* ("small hill"), noun in apposition. Named for the type locality, The Clump, a low hill covered with a clump of tall eucalypt trees. Because the surrounding country is flat and heathy, The Clump has long been a landmark on the northern part of the Tasmanian west coast.

**Remarks.** *L. clivulus* is similar to *L. latus* in gonopod structure but the prefemoral process is shorter, the prefemoral process tip less expanded and the tibiotarsus bent posteriorly at nearly a right angle to the telopodite. The two species co-occur along the coast between the Arthur and Pieman Rivers, and can be distinguished in the field by coloration and by the smoother paranotal margin in *L. clivulus*.

#### *Lissodesmus cognatus* sp. nov.

Figures 25, 26, 27, 69cog, 70cog, 71cog, 76 (map)

*Lissodesmus* sp. NE3.—Mesibov, 1996: 17.—Mesibov, 1997: 567.—Mesibov, 2003a: 209.

**Material examined.** Holotype. Male, Australia, Tasmania. Weavers Creek, EQ330091 ( $41^\circ28'07''S$   $147^\circ23'42''E$ ), 380 m, 31.vii.1994, R. Mesibov & T. Moule, QVM 23:15287.

Paratypes. 2 males, North Esk River, EQ336079 ( $41^\circ28'46''S$   $147^\circ24'08''E$ ), 490 m, 23.ii.1992, R. Mesibov, QVM 23:15284; 2 males, "Elkington" property, EP312979 ( $41^\circ34'11''S$   $147^\circ22'27''E$ ), 350 m, 18.iii.1992, R. Mesibov, AM KS91171 (ex QVM 23:15283); 4

males, same details, QVM 23:15283, 2 dissected; 2 females, Weavers Creek, EQ307122 (41°26'27"S 147°22'02"E), 680 m, 19.vii.1994, R. Mesibov, QVM 23:15289; male, Tower Hill, EP708983 (41°33'49"S 147°50'56"E), 720 m, 31.xii.1998, R. Mesibov & K. Bonham, QVM 23:40758; 10 males, Cocks Creek, EQ767040 (41°30'42"S 147°55'08"E), 480 m, ii.2001, R. Bashford, pitfall sample, QVM 23:24738, 2 dissected.

Other material. 14 males, 2 females and 5 juveniles from "Aplico" property, Cocks Creek, Grants Creek, Long Gully Creek, Musselboro, Rabbity Creek, Tower Hill and Weavers Creek (see "*Lissodesmus* supplement" for details).

**Description.** Male c. 14 mm long,  $H = 1.3$  mm. In alcohol, well-coloured specimens under low magnification near-white in body colour with red tinge transversely near posterior margins of metatergites and dorsa of prozonites. Antennae long, slender (Fig. 69cog), about 2.5× a socket diameter apart. Paranota reduced,  $R = 1.3$  (Fig. 70cog); posterior corners turned up slightly. Legs fairly slender, tarsus about as long as femur, tibia with slight ventral distal swelling (Fig. 71cog). Telopodite (Figs 25, 26, 27) reaching leg 5 when retracted. Solenomere arising at half the telopodite height, directed posterodistally at a small angle to telopodite axis, terminating with toothed subapical collar at about half the prefemoral process height. Tibiotarsus a slightly flattened, bluntly pointed rod about as wide as solenomere but shorter, more or less parallel to solenomere but gradually curving laterally. Femoral process arising proximal to solenomere origin (at about one-third the telopodite length), pressed close to prefemoral process proximally, forked near base; branches more or less equal, blade-like, pointed, the anterior branch directed distally and terminating at level of solenomere tip, the posterior branch curving anteriorly, its tip sometimes lying between anterior branch and prefemoral process. Prefemoral process about half the width of telopodite base, bending posteriorly at about two-thirds its length and tapering, the flexed distal section bearing a comb of c. 15–20 large, irregular, proximally directed teeth. Uncus prominent, arising at about half the prefemoral process length (about the level of the solenomere tip) on well-defined longitudinal ridge near lateral edge of process.

**Distribution and habitat.** An uncommon species known from wet eucalypt forest in two disjunct areas c. 35 km apart in north-east Tasmania (Fig. 76): south and west of Mt Barrow (c. 30 km<sup>2</sup>), and north and east of Tower Hill (c. 15 km<sup>2</sup>).

**Etymology.** Latin *cognatus* ("kindred"), adjective. At first glance, *L. cognatus* seems to be closely related to both *L. alisonae* and *L. hamatus*.

**Remarks.** Furry individuals of *L. cognatus* have been found near the North Esk River, Weavers Creek and Musselboro. Specimens from the "Elkington" property, a few kilometres to the south in the South Esk River catchment, are non-furry, as are all specimens from the Tower Hill portion of the range. I have previously speculated (Mesibov, 1997, 2003a) that *L. cognatus* is a stabilised hybrid of *L. alisonae* and *L. hamatus*, i.e. a product of reticulate evolution. The two putative parents meet with minimal overlap in the western block of the *L. cognatus* range, and *L. hamatus* occurs in the eastern block.

### *Lissodesmus cornutus* sp. nov.

Figures 28, 29, 30, 69cor, 70cor, 71cor, 74 (map)

*Lissodesmus* sp. SW1.—Mesibov, 1996: 18.

**Material examined.** Holotype. Male, Australia, Tasmania. Scotts Peak Dam, DN425343 (43°02'29"S 146°17'38"E), 280 m, pitfall samples WY and WZ collected 12–16.xi.2001, D. Driscoll, QVM 23:45827 (ex QVM 23:24824).

Paratypes. Male, Birchs Inlet, approx. CN753875 (42°33'16"S 145°28'51"E), 18.x.1993, J. Griffith, QVM 23:12036; 2 males, details as for holotype, AM KS91172 (ex QVM 23:24824); 5 males, details as for holotype, QVM 23:24824, 2 dissected; female, W of Strathgordon, DN175655 (42°45'30"S 145°59'30"E), 410 m, 1.x.2003, R. Mesibov, QVM 23:25476.

Other material. 63 males and at least 9 females and juveniles from Acheron Cave area, Darwin, Deadmans Bay, Denison River valley, Edgar Dam, Franklin River valley, Galigne Creek, Gordon River valley, Hibbs Lagoon, Kutikina Cave area, Mt McCutcheon, Olga River valley, Orange River valley, Scotts Peak Dam and Wedge Inlet (see "*Lissodesmus* supplement" for details).

**Description.** Male c. 17 mm long,  $H = 1.6$  mm. In alcohol, most specimens under low magnification near-white, the only pigmentation a red tinge distally on antennae. Antennae long and slender (Fig. 69cor), about 2.25× a socket diameter apart. **Paranota wide, highly modified,  $R = 1.5$  (Fig. 70cor), posterior corners extended as large, upwardly curved, conical structures with ozopore opening midway to tip at anterior end of lateral groove (Fig. 28).** Legs slender, tarsus about as long as femur, tibia with slight ventral distal swelling (Fig. 71cor), sphaerotrichomes lacking on leg 6 femur and prefemur. Telopodite (Figs 29, 30) somewhat sinuous, widening just proximal to prefemoral process origin, with sparse, long setae extending posterolaterally to just distal of tibiotarsus origin, reaching leg 6 when retracted. Solenomere arising at one-third the telopodite height, directed posteriorly at nearly a right angle to telopodite axis, curving distally and laterally, terminating with a small, pointed subapical projection at about one-third the prefemoral process height. Tibiotarsus much wider and somewhat longer than solenomere, directed more or less parallel to solenomere in mesal view but strongly curved laterally, flattened, widening at the apex and terminating in two large, widely spaced, bluntly pointed teeth with 1 or 2 smaller teeth between. Femoral process arising well distal to solenomere origin at about one-quarter the prefemoral process height, blade-like, pressed close at its base to the prefemoral process, directed posterodistally and curving distally and slightly mesally to terminate at two-thirds the prefemoral process height with two small apical teeth, with a large, posterobasally directed branch arising at nearly half the process length. Prefemoral process nearly as wide as telopodite base below solenomere origin, curving mesally, then laterally, then again mesally, flexing slightly posteriorly at about two-thirds its length and tapering slightly to a broad, rounded tip, with a comb of c. 15 long, posterobasally directed teeth on mesal edge of flexed distal section. Uncus large, arising centrally at about half the prefemoral process height (well distal of solenomere tip).

**Distribution and habitat.** Known from wet eucalypt forest and cool temperate rainforest over c. 5000 km<sup>2</sup> in south-west

Tasmania (Fig. 74), from Darwin in the north to Deadmans Bay in the south, east to the Scotts Peak Dam Road, and from sea level to at least 600 m.

*Etymology.* Latin *cornutus* ("horned"), adjective, for the horned shape of the posterior projections of the paranota.

***Lissodesmus devexus* sp. nov.**

Figures 31, 32, 33, 69dev, 70dev, 71dev, 74 (map)

*Lissodesmus* sp. NE2.—Mesibov, 1998: 155.—Mesibov, 1999: 252.

*Material examined.* Holotype. Male, Australia, Tasmania. Lebrina, EQ168424 (41°10'09"S 147°12'00"E), 240 m, 5.i.1993, R. Mesibov, QVM 23:45948 (ex QVM 23:15515).

Paratypes. Male, Rattler Hill, EQ744353 (41°13'48"S 147°53'15"E), 650 m, 29.viii.1990, R. Mesibov, QVM 23:15512, dissected; 2 males, details as for holotype, AM KS91173 (ex QVM 23:15515); 2 males, details as for holotype, QVM 23:15515, 1 dissected; 8 stadium 7 males, 2 stadium 7 females, details as for holotype, QVM 23:15538; 3 females, Retreat, EQ153423 (41°10'13"S 147°10'56"E), 320 m, 2.vii.1993, T. Kingston, QVM 23:21554; 2 males, same details but EQ137463 (41°08'03"S 147°09'47"E), 300 m, QVM 23:21534, 1 dissected; 4 males, Mt Roland, DQ402119 (41°26'31"S 146°17'02"E), 310 m, 5.vi.1994, R. Mesibov, QVM 23:15506, 1 dissected; 8 males, Shepherds Rivulet, EQ217388 (41°12'06"S 147°15'31"E), 150 m, 6.vii.1994, R. Mesibov, QVM 23:15509, 1 dissected; male, Lowes Mount, EP331953 (41°35'35"S 147°23'49"E), 430 m, 5.vii.1995, R. Mesibov, QVM 23:21542, dissected.

Other material. 115 males, 71 females and 45 juveniles from 77 localities (see "*Lissodesmus* supplement" for details).

*Description.* Male c. 12 mm long,  $H = 1.3$  mm. In alcohol, most specimens under low magnification a uniform very pale brown in body colour. Antenna slender (Fig. 69dev). Paranota slightly reduced,  $R = 1.5$  (Fig. 70dev), posterior corners turned up. Legs slender, tarsus about as long as femur (Fig. 71dev), sphaerotrichomes on tibia and tarsus only of leg 6. Telopodite (Figs 31, 32, 33) widest at prefemoral process origin, almost reaching leg 5 when retracted. **Solenomere arising at slightly more than half the telopodite height, directed posterodistally at a large angle (c. 60°) to the telopodite axis, terminating without a subapical process at about two-thirds the telopodite height in a sharp distal bend. Tibiotarsus a somewhat flattened rod slightly larger than solenomere and about as long, straight and directed posterobasally at a large angle (greater than 90°) to the telopodite axis, widening and flattening near the tip and terminating in a sharp mesal bend, the tip sometimes broadly notched, the midsection with numerous annular "wrinkles" (Fig. 31).** Femoral process arising at about the level of solenomere origin, small and blade-like with a somewhat sinuous outline, directed distally, not closely pressed to prefemoral process, terminating at about three-quarters the prefemoral process height (well distal to solenomere tip). Prefemoral process about as wide at its base as the telopodite base, tapering and sharply flexed posteriorly at its midpoint, the tip variably armed with teeth on posterior (proximally facing) surface (Figs 32, 33). Uncus arising on mesal edge of prefemoral process just proximal to flexure in latter, variably large (Figs 32, 33) but typically directed posterodistally and in some forms (see left gonopod in Fig. 31) paired with prefemoral process tip as a major apical feature of telopodite.

*Distribution and habitat.* In wet eucalypt forest and cool temperate rainforest over c. 3000 km<sup>2</sup> in the higher-rainfall parts of northern and north-east Tasmania (Fig. 74), from Browns Creek near Port Sorell east to Weldborough, south to Lowes Mount near Deddington, and from near sea level to at least 900 m. Populations around Mt Roland and Liena are apparently disjunct (Fig. 74), being separated by about 40 km from known *L. devexus* sites in the West Tamar region. *L. devexus* is gregarious and often locally abundant.

*Etymology.* Latin *devexus* ("sloping down"), adjective, for the orientation of the tibiotarsus on the gonopod.

***Lissodesmus dignomontis* sp. nov.**

Figures 34, 35, 69dig, 70dig, 71dig, 78 (map)

*Material examined.* Holotype. Male, Australia, Victoria. "Lapoinya" property, Yarragon South, 38°14'40"S, 146°05'30"E, 360 m, 17.iv.2005, R. Mesibov, NMV K-9663.

Paratypes. Male, west of Allambee, 38°16'55"S 146°00'12"E, 430 m, 30.ix.2004, R. Mesibov & T. Moule, NMV K-9507, dissected; 2 males, details as for holotype, AM KS91428; 8 males, details as for holotype, NMV K-9664 to K-9671, 1 dissected; male, Allambee, 38°16'27"S 146°03'03"E, 450 m, 22.iv.2005, R. Mesibov, NMV K-9682; 2 males, Mt Worth, 38°16'14"S 145°58'54"E, 440 m, 22.iv.2005, R. Mesibov, NMV K-9673 and K-9674.

*Description.* Male c. 15 mm long,  $H = 1.4$  mm. In alcohol, well-coloured specimens under low magnification very pale brown in body colour with two discrete, narrow, transverse bands of red-brown posteriorly on metatergites. Antenna slender (Fig. 69dig). Paranota fairly wide,  $R = 1.5$ , with about 4 posterior marginal teeth (Fig. 70dig), posterior corners not turned up. Legs robust, tarsus slightly longer than femur, tibia with prominent ventral distal swelling (Fig. 71dig). Telopodite (Figs 34, 35) reaching leg 5 when retracted. Solenomere arising at half the telopodite height, directed posterodistally at a small angle to telopodite axis, terminating with small subapical projection at just over half the prefemoral process height. **Tibiotarsus rod-like, directed posterodistally and between one-third and half as long as solenomere.** Femoral process arising distal to solenomere origin at about one-third the prefemoral process height, blade-like, curving slightly anterolaterally and tapering to a blunt point, terminating at about the level of the prefemoral process tip. **Prefemoral process about half as wide at origin as telopodite base, strongly tapering distally, curving posteriorly near tip and terminating in flattened, blunt point.** Uncus prominent, arising at about half the prefemoral process height (just basal to solenomere tip).

*Distribution and habitat.* Known only from wet eucalypt forest at four sites within a c. 25 km<sup>2</sup> area near Mt Worth in West Gippsland (Fig. 78). At three of the four sites *L. dignomontis* co-occurs with *L. gippslandicus*, and at Yarragon South it co-occurs with *L. johnsi*.

*Etymology.* Latin *dignus* ("worthy") + *montis* ("mountain"), noun in apposition. Named for Mt Worth, one of the known localities for this rare species.

*Lissodesmus gippslandicus* sp. nov.

Figures 36, 37, 69gip, 70gip, 71gip, 79 (map)

**Material examined.** Holotype. Male, Australia, Victoria. Mt Fatigue, 38°34'13"S 146°18'25"E, 570 m, 28.ix.2004, R. Mesibov & T. Moule, NMV K-8990.

Paratypes. 2 males, details as for holotype, AM KS91174; male, details as for holotype, NMV K-8991; 6 females, details as for holotype, NMV K-8992 to K-8997; 9 males, 4 females, Loop Track, E of Allambee, 38°15'52"S 146°04'27"E, 440 m, 21.xii.2004, R. Mesibov, NMV K-9483 to K-9495, 2 males dissected.

Other material. 46 males and 12 females from Allambee, Allambee South, Balook, Darlimurla, Mirboo North, Mt Worth, Narracan, Tarra-Bulga National Park, Thorpdale and Yarragon South (see "*Lissodesmus* supplement" for details).

**Description.** Male c. 18 mm long,  $H = 1.6$  mm. In alcohol, well-coloured specimens under low magnification with pale brown body colour, red-purple speckling on metatergites and intense red-purple transverse banding along posterior margins of prozonites. Antenna with relatively large antennomere 6 (Fig. 69gip). Paranota fairly wide with strongly produced anterior "shoulders" and two inconspicuous posterior marginal teeth,  $R = 1.5$  (Fig. 70gip), posterior corners not turned up. Legs robust, tarsus longer than femur, tibia with prominent ventral distal swelling (Fig. 71gip). Telopodite (Figs 36, 37) almost reaching leg 4 when retracted. Solenomere arising at about half the telopodite height, directed distally with a slight posterior curvature, terminating with prominent subapical collar at about half the prefemoral process height. Tibiotarsus origin on posteromesal surface of telopodite, not close to solenomere origin; tibiotarsus a thin, pointed rod directed posterodistally at a small angle to telopodite axis, about one-quarter the length of the solenomere. **Femoral process arising well proximal to solenomere origin, blade-like with a deeply notched tip, curved anteriorly and pressed close basally to prefemoral process, terminating at less than one-quarter the prefemoral process height (well proximal to solenomere tip).** Prefemoral process about half as wide at origin as telopodite base, tapering slightly to mid-length but distally widening and flexing posteromesally, the tip pointed posteromesally, the lateral edge of the process a comb of c. 20 long, mainly posterobasally directed teeth from about two-thirds the process length. Uncus prominent, arising near base of prefemoral process on mesal side, with a widened, deeply notched tip.

**Distribution and habitat.** In wet eucalypt forest in West and South Gippsland (Fig. 79), often locally abundant. The Thorpdale specimens were collected in 1899, before the densely forested Thorpdale area was cleared for farming. The pre-European range of this species may have been as much as 1000 km<sup>2</sup>, but is now possibly only a third of that figure.

**Etymology.** Named for the Gippsland district, the southern and western parts of which are home to this species.

*Lissodesmus hamatus* sp. nov.

Figures 4B, 6B, 38, 39, 69ham, 70ham, 71ham, 77 (map)

*Lissodesmus* sp. E1.—Mesibov, 1994: 134.—Mesibov, 1996: 17.—Mesibov, 1997: 567.—Mesibov, 1999: 252.

**Material examined.** Holotype. Male, Australia, Tasmania. Mt Hobbs, EN476926 (42°31'02"S 147°34'46"E), 580 m, 21.iii.1992, R. Mesibov, QVM 23:45944 (ex QVM 23:16073).

Paratypes. 7 males, details as for holotype, QVM 23:16073; 2 males, details as for holotype, AM KS91175 (ex QVM 23:16073); 4 stadium 7 males, 1 stadium 6 male, 7 females, 1 stadium 7 female, details as for holotype, QVM 23:15966; 4 males, Ringarooma Tier, EQ829796 (40°49'49"S 147°58'59"E), 80 m, 19.ix.1992, R. Mesibov & T. Moule, QVM 23:16076, 2 dissected; 3 pairs *in copula*, same details, QVM 23:16157; 4 females, same details, QVM 23:15845; 9 males, Lagoon of Islands, DP947376 (42°06'48"S 146°56'09"E), 750 m, 5.iii.1995, R. Mesibov, QVM 23:21349, 1 dissected; female, same details, QVM 23:21505.

Other material. 371 males, 382 females and 238 juveniles from 234 localities (see "*Lissodesmus* supplement" for details).

**Description.** Male c. 16 mm long,  $H = 1.7$  mm (see *Remarks*). In alcohol, well-coloured specimens under low magnification with pale brown body colour and light red speckling dorsally on both prozonites and metazonites, more intense medially near posterior margins. Antenna fairly long and slender (Fig. 69ham). Paranota reduced,  $R = 1.3$  (Fig. 70ham), posterior corners slightly turned up (Fig. 4B). Limbus with toothed elements (Fig. 6B). Legs fairly slender, tarsus slightly longer than femur, tibia with slight ventral distal swelling (Fig. 71ham). Epiproct with prominent paired, bluntly rounded projections. Telopodite (Figs 38, 39) reaching leg 5 when retracted. Solenomere arising at about half the telopodite height, directed posterodistally at c. 45° to telopodite axis, terminating with toothed subapical collar at one-third to half the prefemoral process height. Tibiotarsus rod-like, pointed, about two-thirds the solenomere length and apically almost touching solenomere. Femoral process arising at level of solenomere origin, blade-like and anteroposteriorly flattened with a short, shelf-like posterior branch at one-third the process length, bluntly tipped and terminating at half the prefemoral process height, just distal to solenomere tip. **Prefemoral process about two-thirds the width of telopodite base, bending laterally at about two-thirds its height with a prominent "shoulder" process on mesal side of bend, curving posteriorly distal to bend with a variable number of long, mainly posterobasally directed teeth forming a comb on lateral edge of tip.** Uncus prominent, arising centrally at about half the prefemoral process height, with a coarsely toothed outer edge.

**Distribution and habitat.** Common in dry and wet eucalypt forest over c. 16 000 km<sup>2</sup> in eastern Tasmania (Fig. 77), from Ringarooma Tier in the far north-east to Dunalley in the south-east, from the eastern coast (including Maria Island) across the Eastern Tiers and the Midlands to the eastern portion of the Central Plateau, and from sea level to at least 1070 m. In places along the northern edge of its range, *L. hamatus* is parapatric with *L. adrianae* and *L. alisonae* (Mesibov, 1997).

**Etymology.** Latin *hamatus* ("hooked"), adjective, for the upturned corners of the posterior projections of the paranota. The name was suggested by Peter Johns (in litt.), who collected *L. hamatus* near Triabunna in 1972.

**Remarks.** Gonopod form varies over the range of this species. The number of subterminal teeth on the prefemoral process

ranges from 6 to 10, and the width of the flexed tip of the process can be proportionately greater than shown for specimens from the type locality. In the eastern portion of the range the short, posterior branch of the femoral process often has a bluntly forked tip. *H* ranges widely, from c. 1.2 mm in drier and more southerly areas to c. 1.8 mm in wetter and more northerly areas; larger males have markedly more swollen legs.

***Lissodesmus horridomontis* sp. nov.**

Figures 40, 41, 69hor, 70hor, 71hor, 73 (map)

*Lissodesmus* sp. NE5.—Mesibov, 1994: 134.

**Material examined.** Holotype. Male, Australia, Tasmania. Mt Horror, EQ588513 (41°05'14"S 147°42'00"E), 200 m, 24.iv.1993, R. Mesibov, QVM 23:45829 (ex QVM 23:15491);

Paratypes. Male, Friend Creek, EQ862540 (41°03'37"S 148°01'33"E), 150 m, 25.xi.1992, QVM 23:15492; 4 males, Mt Horror, EQ604547 (41°03'23"S 147°43'07"E), 220 m, 18.iii.1993, R. Mesibov, QVM 23:15490; 7 females, same details, QVM 23:15484; 7 males, Speck Creek, EQ566549 (41°03'18"S 147°40'24"E), 290 m, 18.iii.1993, QVM 23:15497; 2 males, details as for holotype, AM KS91176 (ex QVM 23:15491); 2 males, details as for holotype, QVM 23:15491.

Other material. 21 males, 17 females and 5 juveniles from Connors Road, Friend Creek, Martins Hill, Mt Horror, Oxberry Creek, Pearly Brook, Speck Creek and Tomahawk River (see "*Lissodesmus* supplement" for details).

**Description.** Male c. 13 mm long, *H* = 1.2 mm. In alcohol, most specimens under low magnification uniformly near-white. Antenna slender, not strongly clavate (Fig. 69hor). Paranota reduced, *R* = 1.3 (Fig. 70hor), posterior corners slightly turned up. Legs robust, tarsus shorter than femur (Fig. 71hor), sphaerotrichomes lacking on leg 6 femur and prefemur. Epiproct with prominent paired, bluntly rounded projections. Telopodite (Figs 40, 41) reaching leg 5 when retracted. Solenomere arising at one-third to half the telopodite height, directed posterodistally at somewhat less than 45° to telopodite axis, terminating without subapical projection at slightly less than half the prefemoral process height. Tibiotarsus about as large as solenomere but slightly shorter, directed more or less parallel to solenomere, flattened posterobasally and terminating in a variably dentate edge with a small, bluntly pointed subapical projection on anterolateral surface. Femoral process arising at level of solenomere origin, straight, pointed, blade-like, directed distally and terminating at level of solenomere tip. **Prefemoral process about as wide at origin as telopodite base, tapering slightly and bending laterally at about mid-height with a coarsely toothed "shoulder" on the mesal side of bend, curving posteromesally with the tip flexed laterally at almost 180°, the tip bearing a comb of c. 10–15 long, basally directed teeth.** Uncus prominent, arising just proximal to lateral bend in prefemoral process (just distal to solenomere tip), outer edge coarsely dentate.

**Distribution and habitat.** Known from wet eucalypt forest and cool temperate rainforest over c. 150 km<sup>2</sup> in north-east Tasmania (Fig. 73), from Williams Hill east to Old Chum Dam, and from 80 to 650 m. *L. horridomontis* is abundant in the western portion of its small range.

**Etymology.** Latin *horridus* ("frightful") + *montis* ("mountain"), noun in apposition. Named for the type locality, Mt Horror.

***Lissodesmus inopinatus* sp. nov.**

Figures 42, 43, 69ino, 70ino, 71ino, 72 (map)

*Lissodesmus* sp. E2.—Mesibov, 1996: 17.

**Material examined.** Holotype. Male, Australia, Tasmania. Halls Creek, EP660382 (42°06'19"S 147°47'53"E), 540 m, 22.iii.1992, R. Mesibov, QVM 23:45828 (ex QVM 23:16164).

Paratypes. 2 males, details as for holotype, AM KS91177 (ex QVM 23:16164); 7 males, details as for holotype, QVM 23:16164, 2 dissected; 5 females, 1 stadium VII female, details as for holotype, QVM 23:16168; male, Pinnacles Creek, EP528531 (41°58'19"S 147°38'14"E), 520 m, 22.iii.1992, R. Mesibov, QVM 23:16165; male, Mt Ponsonby, EN441966 (42°28'53"S 147°32'11"E), 610 m, 3.ix.2000, R. Mesibov, QVM 23:41984; male, Anglers Creek, EP697230 (42°14'30"S 147°50'41"E), 570 m, 7.x.2001, R. Mesibov & T. Moule, QVM 23:24858.

Other material. 3 males, 16 females and 8 juveniles from Anglers Creek, Mt Mismanagement, Parramores Tier, Pinnacles Creek and Rocka Rivulet (see "*Lissodesmus* supplement" for details).

**Description.** Male c. 17 mm long, *H* = 1.7 mm. In alcohol, well-coloured specimens under low magnification with very pale brown body colour, faintly reddish and more intense medially and posteriorly on metatergites. Antenna long and slender (Fig. 69ino). Paranota reduced, *R* = 1.3 (Fig. 70ino), posterior corners turned up. Legs fairly slender, tarsus shorter than femur, tibia with slight ventral distal swelling (Fig. 71ino). Telopodite (Figs 42, 43) widest at prefemoral process origin, reaching leg 5 when retracted. Solenomere arising at one-third the telopodite length, directed posterodistally at a small angle (c. 30°) to telopodite axis, terminating with toothed subapical collar at just under half the prefemoral process height. Tibiotarsus nearly as thick as solenomere but slightly shorter, directed posterodistally and slightly laterally at acute angle to solenomere, flattened and bluntly pointed. Femoral process arising at level of solenomere origin, forked near base, both branches blade-like, pointed; anterior branch directed distally and pressed close to prefemoral process, terminating at about one-third the prefemoral process height (proximal to solenomere tip); posterior branch smaller than anterior branch, curved anterodistally. **Prefemoral process at base about two-thirds the width of telopodite base proximal to solenomere origin, bending sharply posterolaterally at about two-thirds its height with a large, mesolaterally flattened, broadly toothed projection on mesal edge of prefemoral process at bend, the distal portion of process with c. 10–20 teeth lying at a small angle to process axis, the tip also toothed.** Uncus prominent, arising on mesal edge of prefemoral process at about half the process height (just distal to solenomere tip).

**Distribution and habitat.** An uncommon species in dry and wet eucalypt forest over c. 1000 km<sup>2</sup> in the Eastern Tiers of Tasmania (Fig. 72), from Pinnacles Creek (c. 15 km E of Campbell Town) south to Mt Ponsonby and east to Anglers Creek.

**Etymology.** Latin *inopinatus* ("unexpected"), adjective. While carrying out a Tasmania-wide millipede survey in the 1990s,

the only *Lissodesmus* species I expected to find in the *L. inopinatus* range was *L. hamatus*.

**Remarks.** *L. inopinatus* varies considerably in overall size across its range.

***Lissodesmus johnsi* sp. nov.**

Figures 44, 45, 69joh, 70joh, 71joh, 78 (map)

**Material examined.** Holotype. Male, Australia, Victoria, Uralla Nature Reserve, Trafalgar, 38°13'36"S 146°08'53"E, 140 m, 19.iv.2005, R. Mesibov, NMV K-9682.

Paratypes. Male, near Trafalgar, Gippsland, viii.1890, W. Kershaw, NMV K-9506, dissected; male, "Lapoinya" property, Yarragon South, 38°14'30"S 146°05'34"E, 370 m, 17.iv.2005, R. Mesibov, NMV K-9681; 2 males, details as for holotype, AM KS91429; 10 males, details as for holotype, NMV K-9683 to K-9692, 1 dissected; 9 females, details as for holotype, NMV K-9693 to K-9701.

**Description.** Male c. 14 mm long,  $H = 1.2$  mm. In alcohol, well-coloured specimens under low magnification very pale brown in body colour with red-brown speckling transversely on posterior half of metatergites. Antenna short, moderately slender (Fig. 69joh). Paranota prominent but reduced,  $R = 1.4$ , with 4–5 posterior marginal teeth (Fig. 71joh), posterior corners not turned up. Legs short, robust, tarsus about as long as femur, tibia with prominent ventral distal swelling (Fig. 70joh). Telopodite (Figs 44, 45) posteriorly excavated at base, reaching leg 5 when retracted. Solenomere arising at just over half the telopodite height, directed posterodistally at a small angle to telopodite axis, terminating at somewhat more than half the prefemoral process height with flattened, posterolaterally flexed tip. **Tibiotarsus broad and flattened, a marginally toothed fan in posterior view, directed distally and about half as long as solenomere.** Femoral process arising well distal to solenomere origin at about half the prefemoral process height, blade-like, slightly swollen distally but tapering to a blunt point, terminating distal to prefemoral process tip. **Prefemoral process about half as wide at origin as telopodite base, curving slightly mesally, sharply tapering distally and terminating in a simple blunt point.** Uncus prominent, arising at about two-thirds the prefemoral process height (at about the level of solenomere tip).

**Distribution and habitat.** Known only from wet eucalypt forest in a small area near Trafalgar in West Gippsland (Fig. 78); the two contemporary sites are c. 5 km apart. At the Yarragon South locality, *L. johnsi* co-occurs with *L. dignomontis* and *L. gippslandicus*.

**Etymology.** Named for Peter Johns, formerly of the University of Canterbury (Christchurch, New Zealand), who recognised the distinctiveness of the 1890 specimen and illustrated its gonopod, assigning the species to *Pseudopriopeltis* (*Australopeltis*) without naming it (Johns, 1964).

***Lissodesmus latus* sp. nov.**

Figures 6A, 9, 46, 69lat, 70lat, 71lat, 75 (map)

***Lissodesmus* sp. NW1.**—Mesibov, 1993: 31.—Mesibov, 1996: 18.—Mesibov, 1998: 155.—Bonham et al., 2002: 240.

**Material examined.** Holotype. Male, Australia, Tasmania. Wombat Hill, W of Waratah, CQ703065 (41°28'56"S 145°26'47"E), 670 m, 24.ix.1990, R. Mesibov, QVM 23:17495.

Paratypes. 2 males, Wombat Hill, W of Waratah, CQ702064 (41°29'00"S 145°26'42"E), 680 m, 19.ix.1990, R. Mesibov, AM KS91178 (ex QVM 23:17490); 2 males, same details, QVM 23:17490, 1 dissected; 2 males, same details but 22.ix.1990, QVM 23:17491; 2 males, details as for holotype but 23.ix.1990, QVM 23:17492; 2 males, Wombat Hill, W of Waratah, CQ704066 (41°28'53"S 145°26'51"E), 690 m, 28.ix.1990, R. Mesibov, QVM 23:17496, 1 dissected; male and female *in copula*, same details, QVM 23:17497; 7 females, same details, QVM 23:17547; 2 males, same details but 29.ix.1990, QVM 23:17493; 2 males, same details but 30.ix.1990, QVM 23:17494; 9 males, Montagu Swamp, CQ265620 (40°58'28"S 144°56'16"E), 30 m, 22.vi.1991, R. Mesibov, QVM 23:17499, 1 dissected; 5 males, 2 females, Deep Creek Bay, CQ447787 (40°49'40"S 145°09'29"E), <10 m, 5.ix.2000, K. Bonham, QVM 23:41955, 2 males dissected.

Other material. 186 males, 116 females and 20 juveniles from 105 localities (see "*Lissodesmus* supplement" for details).

**Description.** Male c. 20 mm long,  $H = 1.8$  mm. In alcohol, well-coloured specimens of typical form (see *Remarks*) under low magnification with near-white body colour and wide, transverse, purple banding, interrupted medially, on posterior margin of prozonites. Antenna long (Fig. 69lat). Paranota fairly wide,  $R = 1.5$ , sometimes with two prominent posterior marginal teeth (Fig. 70lat), posterior corners not turned up (Fig. 9). Limbus elements simple, tapering to point (Fig. 6A). Legs robust, tarsus longer than femur, tibia with slight ventral distal swelling (Fig. 71lat). Telopodite (Fig. 46) reaching leg 5 when retracted. Solenomere arising between one-quarter and one-third the telopodite height, directed posterodistally at c. 30° to telopodite axis, curving laterally, terminating with toothed sub-apical collar at about one-third the prefemoral process height. Tibiotarsus wider than solenomere and slightly longer, curving more sharply laterally, diverging from solenomere at a small angle, terminating in a thin, dentate edge sometimes turned anterodistally at level of solenomere tip. Femoral process arising slightly distal to solenomere origin, forked at about one-third its length, both branches blade-like, bluntly pointed; anterior branch closely pressed to prefemoral process at its base, terminating at level of solenomere tip; posterior branch typically as long as or slightly longer than anterior branch, curved anterodistally. Prefemoral process at its origin about two-thirds as wide as telopodite base, very slightly bent laterally, bending posteriorly at just over half its length, the mesal edge and expanded, mesolaterally flattened tip both crenulate or shortly toothed. Two small unci arising at just under half the prefemoral process height (just distal to solenomere tip), one central and one on mesal edge of process.

**Distribution and habitat.** In cool temperate rainforest, wet eucalypt forest and coastal scrub and blackwood/tea-tree forest over c. 13 000 km<sup>2</sup> in north-west Tasmania (Fig. 75), from the Hunter Group of islands to the Franklin River, from the west coast inland to the Leven River and the Cradle Mountain area, and from sea level to at least 950 m. *L. latus* has been found in caves at Gunns Plains, Loongana, Mt Cripps and the Wilson River. It co-occurs with *L. perporosus* over most of its range

and is typically less abundant than *L. perporosus* when the two are syntopic.

**Etymology.** Latin *latus* ("broad, wide"), for the wide and relatively flat paranota.

**Remarks.** Besides the inland form of *L. latus*, represented by the holotype, there is a distinctive coastal form with almost uniformly pale brown to chestnut-brown coloration and with stronger dorsal curvature of the paranota. Despite the striking difference in overall appearance of the two *L. latus* forms, the gonopods of coastal and inland forms in the far north-west are almost indistinguishable. The coastal form occurs close to the western and Bass Strait coasts and in the Hunter Group of islands. I have not yet found a site in the far north-west of Tasmania where the coastal and inland forms co-occur. Coastal *L. latus* closely resembles *L. perporosus*, but females and juveniles of the two species can be separated by inspection of the ozopores (i.e., the pore formula in *L. latus* is normal).

Inland *L. latus* vary in the height of the paranotal margins relative to the body axis, in the sharpness of notches on the lateral edge of the paranota, and in the clear presence or near-absence of a pair of rounded teeth on the posterior margin of each paranotum. On the gonopod telopodite, the anterior branch of the femoral process varies from nearly straight to arc-like (concave posteriorly), and the tip of the tibiotarsus can be straight or upturned. Furry specimens of *L. latus* have been found in the Mt Cripps area and at Lake Lea and the nearby Vale of Belvoir (Fig. 9).

***Lissodesmus macedonensis* sp. nov.**

Figures 47, 48, 69mac, 70mac, 71mac, 79 (map)

**Material examined.** Holotype. Male, Australia, Victoria. Mt Macedon, 37°22'42"S 144°36'35"E, 880 m, 10.ix.2004, R. Mesibov & T. Moule, NMV K-9527.

Paratypes. 2 males, Mt Macedon, 22.x.1963, A. Neboiss, NMV K-9508, K-9509; 2 males, details as for holotype, AM KS91179; 15 males, 1 female, details as for holotype, includes male and female in copula, NMV K-9511 to K-9526, 2 males dissected; 9 females, details as for holotype, NMV K-9528 to K-9536; male, 1 km NE of Blakeville, 37°29'45"S 144°13'07"E, 680 m, 10.ix.2004, R. Mesibov & T. Moule, NMV K-9510.

**Description.** Male c. 17 mm long,  $H = 1.5$  mm. In alcohol, well-coloured specimens under low magnification with very pale brown body colour and red speckling on metatergites, more intense medially and in a transverse band close to posterior metatergal margin. Antenna short, stout (Fig. 69mac). Paranota fairly wide,  $R = 1.5$ , with several indistinct posterior marginal teeth (Fig. 70mac), posterior corners not turned up. Legs short, robust, tarsus about as long as femur, tibia with slight ventral distal swelling (Fig. 71mac). Telopodite (Figs 47, 48) reaching leg 5 when retracted. Solenomere arising at one-third to half the telopodite height, directed posterodistally at c. 45° to telopodite axis, terminating with small, pointed sub-apical projection at one-quarter to one-third the prefemoral process height. Tibiotarsus strongly flattened anteroposteriorly, about as long as solenomere but diverging from it slightly, the expanded tip curling back anterodistally. Femoral process arising distal to solenomere origin at about one-quarter the

prefemoral process height, blade-like, wide, pressed close to prefemoral process at base, deeply notched distally with rounded tips, terminating at just under half the height of prefemoral process. **Prefemoral process at its origin about half as wide as telopodite base, slightly tapered, curving posteromesally at about two-thirds its length, the lateral edge of the distal half a comb of c. 25 long, mainly basally directed teeth, the process tip turned back nearly 180°.** Uncus large, arising from mesal edge of prefemoral process at about one-third the process height (just distal to solenomere tip).

**Distribution and habitat.** Known from wet eucalypt forest at two localities c. 30 km apart: the upper slopes of Mt Macedon, where it is abundant, and near Blakeville in the southern portion of the Wombat State Forest (Fig. 79).

**Etymology.** Named for the type locality, 55 km north-west of Melbourne.

***Lissodesmus martini* (Carl, 1902)**

Figures 49, 50, 69mar, 70mar, 71mar, 79 (map)

*Pseudoprionopeltis martini* Carl, 1902: 599.—Brolemann, 1916: 541.—Chamberlin, 1920: 133.—Verhoeff, 1932: 1982.—Attems, 1940: 453.

*Pseudoprionopeltis (Australopeltis) martini* Johns, 1964: 47.

*Lissodesmus martini* Jeekel, 1983: 150.—Jeekel, 1984: 86.

**Material examined.** Holotype (not seen). Male, Australia, Victoria. Melbourne, date of collection unknown, collected by "Consul Martin", deposited in the Muséum d'Histoire Naturelle in Geneva. According to Johns (1964: 47), who re-illustrated the gonopod of the type, the holotype body has been lost and only a slide mount of the gonopods remains.

Paratypes. None designated.

Other material. 50 males, 19 females and 8 juveniles from Acheron Gap, "The Beeches" near Marysville, Belgrave West, the Bennis Plains area NE of Licola, Coalville, Cockatoo Creek, Emerald, Erica, Gembrook, the Latrobe River near Powelltown, Mt Observation, Narracan, Narracan East, Neerim, Noojee, Sherbrooke Forest, Slippery Hill N of Dargo, Starvation Creek NE of Warburton, Toolangi, Yallourn North and Yinnar (see "*Lissodesmus* supplement" for details). I have not examined the male from Ferntree Gully National Park described by Jeekel (1983).

**Description.** Male c. 18 mm long,  $H = 1.6$  mm. In alcohol, well-coloured specimens under low magnification with pale brown body colour, red speckling anteriorly on metatergites and a red transverse band posteriorly on prozonites, paranota near-white. Antenna moderately long (Fig. 69mar). Paranota fairly wide,  $R = 1.5$ , with about 3 posterior marginal teeth (Fig. 70mar), posterior corners not turned up. Legs robust, tarsus longer than femur, tibia with prominent ventral distal swelling (Fig. 71mar). Telopodite (Figs 49, 50) almost reaching leg 5 when retracted. Solenomere arising at about half the telopodite height, directed posterodistally at a small angle (c. 30°) to telopodite axis, terminating with toothed subapical collar at just under half the prefemoral process height. Tibiotarsus origin on posteromesal surface of telopodite, not close to solenomere origin; tibiotarsus a thin, pointed rod almost parallel to solenomere but curving anterodistally, about half the length of



the solenomere. **Femoral process arising at level of solenomere origin, a massive, wide, bluntly pointed blade directed distally, close to prefemoral process, terminating at just over half the prefemoral process height (distal to solenomere tip). Prefemoral process at its base about half as wide as telopodite base, curving slightly mesally at half its height, bent posteromesally at about three-quarters its length, the tip expanded and dentate on its posterior-facing edge.** Uncus prominent, arising near mesal edge of prefemoral process at just under half the process height (at same level as solenomere tip), with inconspicuously dentate outer edge.

*Distribution and habitat.* In dry and wet eucalypt forest and cool temperate rainforest in the Central Highlands and parts of Gippsland. To judge from earlier records, *L. martini* once ranged east and north-east from Melbourne for ca. 200 km, and it is still Victoria's most widely distributed *Lissodesmus* species (Fig. 79). It is abundant in the Yarra Ranges and occurs up to at least 1120 m elevation.

*Remarks.* Carl (1902) characterised *Pseudoprionopeltis* as having 21 segments behind the head, rather than the expected 19 or 20. The correct number, 20, was first given by Johns (1964) for *L. martini*. Enghoff et al. (1993: 148) suggested that Carl's "21" may have been a typographical error.

Chamberlin (1920) gave *Polydesmus (Oxyurus) serratus* Hutton, 1877 as a synonym of *P. martini*, and listed the type locality of *serratus*, Dunedin in New Zealand, as the only *P. martini* locality. This was clearly an error, as Chamberlin (1920: 133) also claimed that both the identity and generic placement of *P. serratus* were impossible to determine.

This is the fourth time *L. martini* has been described and illustrated, and I am contributing little new other than a scanning electron micrograph of the gonopods. *L. martini* varies only slightly over most of its range, but specimens from the east of that range are smaller and paler than those from the west.

### *Lissodesmus milledgei* sp. nov.

Figures 51, 69mil, 70mil, 71mil, 78 (map)

*Material examined.* Holotype. Male, Australia, Victoria. Myrtle Gully Reserve, 3.4 km WSW of Mt Donna Buang, 37°43'S 145°38'30"E, pitfall emptied 20.i.1995, G. Milledge, ex sample NOH-1840, NMV K-9604.

Paratypes. Male, details as for holotype but 7.iv.1995, ex sample NOH-1841, NMV K-9605; male, Acheron Gap, 6 km NE of Mt Donna Buang, 37°40'43"S 145°44'20"E, pitfall emptied 28.xii.1995, G. Milledge, sample NOH-1851, NMV K-9606, dissected.

Other material. Male, The Beeches, 37°28'S, 145°49'E, 25.iii.1991, M.S. Harvey & M.E. Blofeld, *Nothofagus* litter, WAM T66223.

*Description.* Male c. 14 mm long,  $H = 1.3$  mm. In alcohol, under low magnification with uniformly very pale brown body colour. Antenna short (Fig. 69mil). Paranota reduced,  $R = 1.4$ , anterior shoulders squared rather than rounded (Fig. 70mil), posterior corners slightly turned up. Legs moderately robust, tarsus shorter than femur, tibia with slight ventral distal swelling, sphaerotrachomes on tibia and tarsus only of leg 6 (Fig. 71mil). Telopodite (Fig. 51) reaching leg 5 when retracted. Solenomere arising at half the telopodite height,

directed posterobasally at large angle to telopodite axis but bending at about one-third the process length distally and slightly mesally, terminating with small subapical projection at between one-third and half the prefemoral process height. Tibiotarsus origin on posteromesal surface of telopodite, not close to solenomere origin; tibiotarsus a posterobasally flattened triangular plate with a bluntly pointed tip, directed at c. 45° to telopodite axis, about one-third the solenomere length. Femoral process arising at level of solenomere origin, directed distally and pressed close to prefemoral process, blade-like with a slight anterior shoulder distally, tip rounded, terminating at one-third to half the prefemoral process height (at level of solenomere tip). **Prefemoral process somewhat narrower than telopodite base, tapering, the distal one-third curving posterobasally and slightly mesally and bearing a comb of c. 15–20 long, mainly basally directed teeth; a cluster of three small tooth-like projections on mesal edge of prefemoral process at about two-thirds the process height.** Uncus prominent, arising at level of solenomere and femoral process tips towards lateral edge of prefemoral process.

*Distribution and habitat.* Known from three localities in cool temperate rainforest in the Yarra Ranges east of Melbourne (Fig. 78).

*Etymology.* Named for Graham Milledge, who collected this and many other interesting invertebrate species in the mid-1990s from *Nothofagus* forest in Victoria.

*Lissodesmus modestus* Chamberlin, 1920

Figures 4A, 5A, 7A, 8A, 52, 53, 69mod, 70mod, 71mod, 73 (map)

*Lissodesmus modestus* Chamberlin, 1920: 135.—Attems, 1940: 490.—Jeekel, 1970: 336.—Jeekel, 1984: 91.

*Material examined.* Holotype. Male, Australia, Tasmania. Russell Falls, G.H. Hardy, MCZ 4644. The type is in three pieces but is otherwise in excellent condition. An accompanying label reads "Jan 1915 Russell Falls".

Paratypes. Female, details as for holotype, MCZ 4645.

Other material. 57 males, 82 females and 32 juveniles from Arve Road, Bracken Ridge, Collins Cap, Coopers Creek, Dromedary Creek, Edwards Road, Espies Craig, Fortescue Bay, Gold Creek, Hastings Caves, Ida Bay cave IB-51, Judds Creek, Kallista Creek, Little Florentine River, Mt Clark, Mt Field National Park, Mt Mangana (Bruny Island), Mt Misery, Mt Wellington, Myrtle Forest Creek, Needles Picnic Area, Pelham Tier, Pendulum Palace Cave (Precipitous Bluff), Picton River, Plenty River and Tobys Hill (see "*Lissodesmus* supplement" for details).

*Description.* Male c. 16 mm long,  $H = 1.4$  mm. In alcohol, well-coloured specimens under low magnification very light brown in body colour, with fairly uniform red speckling across metatergites and in a transverse band posteriorly on prozonites. Antenna long, fairly slender (Fig. 69mod). Paranota fairly wide,  $R = 1.5$  (Fig. 70mod), posterior corners not turned up (Fig. 4A) but projecting slightly outwards in most specimens (see also Jeekel, 1984: 93, Fig. 1). Legs robust, tarsus slightly shorter than femur, tibia with prominent ventral distal swelling (Fig. 71mod). Telopodite (Figs 52, 53) reaching leg 4 when retracted. [Note: the convention adopted here of labelling as

“mesal” a telopodite view centred on the solenomere is particularly misleading for this species. As seen in Fig. 52, the solenomere origin is on the anterior surface of the telopodite in situ.] Solenomere arising at about half the telopodite height, directed basally at about 45° to telopodite axis but gradually curving distally, terminating with a small subapical projection at just under half the prefemoral process height. Tibiotarsus rod-like, pointed, directed more or less parallel to solenomere, about one-third the length of solenomere and much thinner. **Femoral process arising distal to solenomere origin, large, blade-like with expanded, leaf-shaped tip, curving posteromesally and terminating just proximal to tip of prefemoral process. Prefemoral process at origin about two-thirds as wide as telopodite base, at about half-length tapering rapidly and bending posteromesally, then bending distally, the last one-third straight, with a row of short, mainly posterodistally and mesodistally directed teeth on mesal edge.** Uncus identification uncertain; possibly represented by low, pointed ridge on prefemoral process at about the level of solenomere tip.

*Distribution and habitat.* In wet eucalypt forest and cool temperate rainforest over c. 4500 km<sup>2</sup> in southern and south-east Tasmania (Fig. 73), from Pelham to the south coast, from the Little Florentine River east to the Channel district, and from near sea level to at least 940 m. *L. modestus* also occurs on South Bruny Island and the Tasman Peninsula, but has not yet been recorded on either North Bruny Island or Forestier Peninsula. It occurs in caves at Ida Bay and Precipitous Bluff. *L. modestus* is hard to find in many parts of its range.

*Remarks.* As noted in the Introduction, there are minor errors with the antennomeres and sphaerotrichomes in the description given by Jeekel (1984). The gonopod coxae are also said (Jeekel, 1984: 93) to be “solidly connected”, which suggests “fused”; they are in fact separate and lightly joined at only one point, as in all *Lissodesmus* species. Jeekel’s description is otherwise accurate and very detailed.

*Lissodesmus montanus* sp. nov.

Figures 54, 55, 69mon, 70mon, 71mon, 73 (map)

*Material examined.* Holotype. Male, Australia, Tasmania. Lake Lea, DP083989 (41°33′22″S 145°54′01″E), 950 m, 18.xii.1993, R. Mesibov & T. Moule, QVM 23:17717.

Paratypes. Male, Algonkian Mountain, approx. DP220059 (42°23′42″S 146°03′08″E), 1020 m, 26.ii.1987, S.J. Smith, ex WHA sample ML011, QVM 23:17715, dissected; female, same details, QVM 23:17714; male, Algonkian Mountain, approx. DP229067 (42°23′16″S 146°03′48″E), 1020 m, 26.ii.1987, S.J. Smith, ex WHA sample ML005, QVM 23:17716, dissected; male, same details, AM KS91180; female, Squires Creek, DP240255 (42°13′07″S 146°04′44″E), 650 m, 16.ii.1994, R. Mesibov, QVM 23:40813; male, Mt Murchison summit, CP850703 (41°48′38″S 145°36′55″E), 1250 m, 11.iv.1998, R. van Riet & B. Dudman, QVM 23:40744.

*Description.* Male c. 23 mm long,  $H = 2.4$  mm. In alcohol, well-coloured specimens under low magnification an almost uniform light red-brown in body colour (unusually, extending to legs and antennae) with small pale brown patches medially and anteriorly on metatergites, and laterally on paranota.

Antenna fairly short, fairly slender (Fig. 69mon). Paranota fairly wide,  $R = 1.5$  (Fig. 70mon), posterior corners not turned up. Legs robust, tarsus longer than femur (Fig. 71mon). Telopodite (Figs 54, 55) narrowing sharply at prefemoral process origin, reaching leg 5 when retracted. Solenomere arising at one-third to half the telopodite height, directed basally at c. 45° to telopodite axis, curving gradually distally, terminating with a toothed subapical collar at about one-third the prefemoral process height. **Tibiotarsus as large as solenomere but diverging from it and curving laterally, greatly expanding apically and deeply and broadly notched, thus terminating in two large spine-like structures.** Femoral process arising just distal to solenomere origin, blade-like with a slight posterior shoulder apically, pressed close to prefemoral process, terminating at about half the prefemoral process height (distal to solenomere tip). **Prefemoral process at origin about half as wide as telopodite base, bending first mesally then distally, the tip curving posteriorly with a comb of c. 20 long, mainly posterobasally teeth on mesal edge, the comb continued proximally as a row of more irregular “saw-teeth” to about the level of solenomere tip.** Uncus small, arising centrally just proximal to solenomere tip.

*Distribution and habitat.* Known from four localities over a range of c. 500 km<sup>2</sup> in central western Tasmania (Fig. 73), from 650 to 1250 m. At Algonkian Mountain, Lake Lea and Squires Creek the habitat was cool temperate rainforest, while on Mt Murchison *L. montanus* was found walking by day among bare rocks (R. van Riet, pers. comm.).

*Etymology.* Latin *montanus* (“of mountains”), adjective.

*Lissodesmus orarius* sp. nov.

Figures 8B, 56, 57, 69ora, 70ora, 71ora, 76 (map)

*Material examined.* Holotype. Male, Australia, Tasmania. Foam Creek, CP255877 (41°38′35″S 144°54′16″E), <10 m, 1.vi.1993, R. Mesibov, QVM 23:45822 (ex QVM 23:17693).

Paratypes. 10 males, Pedder River, CQ150149 (41°23′45″S 144°47′13″E), <10 m, 23.i.1991, R. Mesibov, QVM 23:17683, 2 dissected; 2 males, details as for holotype, AM KS91181 (ex QVM 23:17693); 9 males, details as for holotype, QVM 23:1769, 2 dissected; 3; 18 females, 2 stadium VI juvenile females, details as for holotype, QVM 23:17704.

Other material. 28 males, 53 females and 20 juveniles from Chimney Creek, Foam Creek, Hunters Creek, Interview River, Lanes Tor, Monster Creek, Pedder River, Pieman Head, Rocky Creek, Rupert Point, Sandy Cape and Sea Devil Rivulet (see “*Lissodesmus* supplement” for details).

*Description.* Male c. 17 mm long,  $H = 1.5$  mm. In alcohol, well-coloured specimens under low magnification with almost uniform light brown body colour, somewhat darker posteriorly on prozonites and lighter on paranotal edges. Antenna short, fairly stout (Fig. 69ora). Paranota reduced,  $R = 1.4$  (Fig. 70ora), posterior corners not turned up. Legs moderately robust, tarsus much longer than femur, tibia with slight ventral distal swelling (Fig. 71ora), sphaerotrichomes lacking on leg 6 prefemur (Fig. 8B). Telopodite (Figs 56, 57) reaching just past leg 6 when retracted. Solenomere arising at about one-third the telopodite height, directed posterodistally at c. 45° to telopodite axis,

sharply curving distally and laterally at midpoint, terminating with small subapical projection at about one-third the prefemoral process height. Tibiotarsus about as large as solenomere and paralleling its course, the tip turned distally and bluntly pointed, terminating just proximal to solenomere tip. Femoral process arising distal to solenomere origin, blade-like and slightly expanded in middle, directed distally and pressed close to prefemoral process, bluntly pointed and terminating at about two-thirds the prefemoral process height (distal to solenomere tip). **Prefemoral process as wide as telopodite base, slightly curved laterally, the tip wide, greatly flattened and concave posteriorly, few small teeth on posterior edge of lateral rim, the mesal rim bearing (a) at the process tip a long, more or less cylindrical branch curving posterolaterally, (b) a smaller, finger-like branch directed posterodistally more proximally, and (c) a sharp triangular point at about the level of the femoral process tip.** Uncus small, arising near mesal edge of prefemoral process at level of solenomere tip.

**Distribution and habitat.** Known from a c. 30 km strip along the west coast of Tasmania (Fig. 76), from the Pedder River (just north of Sandy Cape) to the mouth of the Pieman River. Along this strip, *L. orarius* has been found just above sea level in dune scrubs, tea-tree forest and tea-tree scrub. Remarkably, the *L. orarius* distribution extends down to the high tide line, and at the type locality this species was found together with intertidal crabs under driftwood surrounded by sedge and grass. At most of its known localities *L. orarius* is abundant.

**Etymology.** Latin *orarius* ("of the coast"), adjective.

**Remarks.** The number and size of teeth on the lateral branch of the prefemoral process vary a little across the *L. orarius* range.

***Lissodesmus otwayensis* sp. nov.**

Figures 58, 59, 69otw, 70otw, 71otw, 79 (map)

**Material examined.** Holotype. Male, Australia, Victoria, Calder Ridge, 38°42'41"S 143°34'03"E, 380 m, 13.xii.2003, R. Mesibov & T. Moule, NMV K-9614.

Paratypes. Male, 2 miles W of Apollo Bay, 8.iii.1975, M. Campbell, NMV K-9607; 1 stadium 7 male, 1 female, 2 stadium 7 females, Aire Crossing Track, 0.5 km N of Aire R crossing, 38°40'S 143°29'E, 31.i.1995, G. Milledge, direct search, sample NOH-1086, NMV K-9608 to K-9611; 2 males, Turtons Pass, 38°38'43"S 143°40'36"E, 420 m, 12.xii.2003, R. Mesibov & T. Moule, NMV K-9612, K-9613, 1 dissected; 2 males, same details, AM KS91182; 2 males, details as for holotype, NMV K-9618, K-9619, 1 dissected; 3 females, details as for holotype, NMV K-9615 to K-9617; 7 males, Cape Horn, 38°44'13"S 143°34'30"E, 280 m, 13.xii.2003, R. Mesibov & T. Moule, NMV K-9620 to K-9626, 2 dissected; 2 males, 1 female, Diamond Hill, 38°27'05"S 143°56'10"E, 360 m, 14.xii.2003, R. Mesibov & T. Moule, NMV K-9627 to K-9629, 1 male dissected; male, same details but 38°27'00"S 143°56'14"E, NMV K-9630.

**Description.** Male c. 17 mm long,  $H = 1.6$  mm. In alcohol, well-coloured specimens under low magnification pale brown in body colour with red speckling dorsally on prozonites and metatergites, and a darker, transverse red band posteriorly on metatergites. Antennae short, clavate (Fig. 69otw), about 1.75× a socket diameter apart. Paranota reduced,  $R = 1.4$  (Fig. 70otw),

posterior corners not turned up. Legs robust, tarsus longer than femur, tibia with prominent ventral distal swelling (Fig. 71otw). Telopodite (Figs 58, 59) reaching leg 5 when retracted, with posterolateral row of sparse long setae running well distal to process origins, the base posteriorly somewhat excavate just below process origins. Solenomere arising at one-third the telopodite height, directed posterodistally at c. 45° to telopodite axis, curving very slightly laterally, terminating with small subapical projection at just under one-third the prefemoral process height. Tibiotarsus rod-like, bluntly pointed, more or less parallel to solenomere but somewhat narrower and about half its length. **Femoral process arising distal to solenomere origin, blade-like, forked at about half its length, both branches wide and apically pointed; anterior branch curving anteriorly and terminating at about one-third the prefemoral process height (just distal to solenomere tip); posterior branch directed posterodistally and curving slightly mesally. Prefemoral process curving slightly laterally, narrowing and curving posteriorly and distally at just over half the process height, with a sharply pointed "shoulder" on the mesal edge marking the bend, distally bending sharply mesally and tapering to blunt point, almost the whole of the lateral edge distal to the bend a comb of c. 30–40 long, straight teeth.** Uncus arising at just under half the prefemoral process height (distal to solenomere tip) on mesal edge of process.

**Distribution and habitat.** In wet eucalypt forest and cool temperate rainforest in the Otway Ranges (Fig. 79).

**Etymology.** Named for the Otway Ranges, where this species appears to be abundant.

***Lissodesmus peninsulensis* sp. nov.**

Figures 60, 61, 69pen, 70pen, 71pen, 72 (map)

*Lissodesmus* sp. Pl.—Mesibov, 1996: 18.

**Material examined.** Holotype. Male, Australia, Tasmania, Fortescue Bay, EN762228 (43°08'36"S 147°56'13"E), 120 m, 11.iii.1992, R. Mesibov, QVM 23:45825 (ex QVM 23:16173).

Paratypes. Male, Griffiths Road, Koonya State Forest, approx. EN650270 (43°06'S 147°47'E), 19.xi.1977, J.L. Hickman, QVM 23:16170, dissected; male, details as for holotype, AM KS91183 (ex QVM 23:16173); male, details as for holotype, QVM 23:16173, dissected; male, Browns Creek, EN736463 (42°55'56"S 147°54'07"E), 190 m, 20.iii.1992, R. Mesibov, QVM 23:16172, dissected; stadium 7 male, stadium 6 male, 5 stadium 7 females, 2 stadium 6 females, same details, QVM 23:16175; male, Wellard Rivulet, EN730456 (42°56'18"S 147°53'40"E), 140 m, 24.ii.1993, R. Mesibov, QVM 23:16171, dissected; stadium 6 male, female, stadium 7 female, stadium 6 female, same details, QVM 23:16174; male, Mt Clark, approx. EN638267 (43°06'34"S 147°47'02"E), 250 m, 4.v.2002, K. Bonham, QVM 23:25021.

**Description.** Male c. 16 mm long,  $H = 1.6$  mm. In alcohol, well-coloured specimens under low magnification pale to light brown in body colour, somewhat darker posteriorly on prozonites. Antennae long (Fig. 69pen), about 2.5× a socket diameter apart. Paranota wide,  $R = 1.6$  (Fig. 70pen), anterior "shoulders" projecting forward, posterior corners not turned up. Legs long, moderately robust, tarsus slightly longer than femur, tibia

with slight ventral distal swelling (Fig. 71per). Telopodite (Figs 60, 61) almost reaching leg 5 when retracted. **Solenomere arising at just under half the telopodite height, directed posterodistally at c. 45° to telopodite axis, twisted slightly helically, the tip bending distally, terminating with no subapical projection at half the prefemoral process height.** Tibiotarsus unusually wide at base, initially parallel to solenomere but curving posterolaterally, then mesally, then distally; somewhat shorter than solenomere and terminating proximal to solenomere tip. **Femoral process arising just proximal to solenomere origin, blade-like, forked at about one-quarter its length and not pressed close to prefemoral process, the two branches apically pointed and about equal in size; anterior branch curved anteriorly, then distally, approaching prefemoral process apically; posterior branch arcuate, concave anteriorly, bent more strongly anteriorly near tip; the two branches terminating at the level of solenomere tip.** Prefemoral process at origin about two-thirds as wide as telopodite base, sharply narrowing at about one-third its length, the distal two-thirds gradually curving posteriorly, the tip mesolaterally flattened and not armed with teeth. Uncus large, arising laterally at level of solenomere tip, flattened posterobasally, the outer edge slightly crenulate.

**Distribution and habitat.** Known from wet eucalypt forest to 250 m elevation on Forestier and Tasman Peninsulas in south-east Tasmania (Fig. 72). *L. peninsulensis* appears to be uncommon and may have a total range of less than 200 km<sup>2</sup>.

**Etymology.** Latin *peninsula* + *-ensis*, adjective, referring to the Forestier and Tasman Peninsulas.

#### *Lissodesmus perporosus* Jeekel, 1984

Figures 1, 10, 62, 63, 69per, 70per, 71per, 72 (map)

*Lissodesmus perporosus* Jeekel, 1984: 98.

**Material examined.** Holotype (not seen). Male, Australia, Tasmania. Hellyer Gorge, 32 km SSW of Somerset, 25.xi.1980, C.A.W. Jeekel and A. Jeekel-Rijvers. The type is said to be deposited in TM (Jeekel, 1984: 86), but has not yet been received there.

Paratypes. 6 males, 13 females, 3 stadium 7 males, 2 stadium 7 females, details as for holotype; male, 12 km SW of Derwent Bridge, 26.xi.1980, C.A.W. Jeekel and A. Jeekel-Rijvers; 2 males, 4 females, Lake St Clair National Park, near Cynthia Bay, 5 km WNW of Derwent Bridge, 26.xi.1980, C.A.W. Jeekel and A. Jeekel-Rijvers. These specimens are listed as paratypes by Jeekel (1984: 98) but their present locations are unknown and they have not been examined.

Other material. 550 males, 616 females and 328 juveniles from 333 localities (see "*Lissodesmus* supplement" for details).

**Description.** Male c. 18 mm long, *H* = 1.7 mm. In alcohol, under low magnification with near-white body colour and three transverse bands dorsally: reddish purple posteriorly on pronotites, red speckling anteriorly and light brown (mainly medially) posteriorly on metatergites. Antenna fairly short, stout (Fig. 69per). Paranota fairly wide, *R* = 1.5 (Figs 10D, 70per), posterior corners not turned up (Fig. 1). **Pore formula 5, 7, 9–19 in males and females.** Legs robust, tarsus about as long as femur, tibia with slight ventral distal swelling (Fig. 71per). Telopodite (Figs 62, 63) reaching leg 5 when retracted. Solenomere arising at about one-third the telopodite height,

directed posterodistally at a small angle (c. 30°) to telopodite axis, curving slightly laterally, terminating with toothed subapical collar at about one-third the prefemoral process height. Tibiotarsus somewhat larger than solenomere, directed at larger angle to telopodite axis, straight with tip bent anterodistally at a right angle. Femoral process arising just proximal to solenomere origin, blade-like, forked at about one-third its length; anterior branch directed distally, pointed, pressed close to prefemoral process, terminating at just over half the prefemoral process height (distal to solenomere tip); posterior branch about one-quarter as long as anterior branch and much narrower, directed posteriorly and curving slightly distally. Prefemoral process at origin about half the width of telopodite base, curving gradually posteriorly from about half the process height, the mesal edge distally with a few low, tooth-like projections. Small paired unci arising at about half the prefemoral process height (distal to solenomere tip) from middle of posterior surface and from mesal edge.

**Distribution and habitat.** In cool temperate rainforest, wet eucalypt forest, blackwood/tea-tree swamp forest and subalpine woodland over at least 20 000 km<sup>2</sup> in north-west Tasmania (Fig. 72), from sea level to at least 1150 m. The *L. perporosus* range extends from the west coast near Pieman Head to the eastern edge of the Central Plateau and to Notley Gorge in the West Tamar region, and from the Bass Strait coast near the Black River mouth to Tarraleah in the upper Derwent Valley. *L. perporosus* is the most abundant dalodesmid over most of its range. It occurs in *Pinus radiata* plantations (Bonham et al., 2002; Mesibov, 2005) as well as native vegetation and has been found in caves at Bubs Hill and Mole Creek.

**Remarks.** Size and coloration vary little in this species, and females and juveniles are easily recognised by the unusual pore formula. A single male *L. perporosus* from Trackham Creek near Waratah (QVM 23:17460) has a normal pore formula. Another 114 specimens from the same locality, including 28 males, have the *perporosus* formula, indicating that this Trackham Creek male is unique and not representative of a pore-formula "race" within the species. Gonopod structure also varies very little in *L. perporosus*, the gonopods of males from sites 200 km apart at Rebecca Creek and Dee Lagoon differing only slightly in size, number and position of teeth on the prefemoral process. The greatest deviation from the typical *perporosus* gonopod structure is found in the vicinity of Maggs Mountain in the upper Mersey River catchment. Males in this small area have additional tooth-like projections on the prefemoral process, and the tip of the process is thickened and bent over (Fig. 63).

#### *Lissodesmus plomleyi* sp. nov.

Figures 64, 69plo, 70plo, 71plo, 76 (map)

*Lissodesmus* sp. NE4.—Mesibov, 1996: 16.—Mesibov, 1998: 155.

**Material examined.** Holotype. Male, Australia, Tasmania. East of Rattler Hill, EQ743353 (41°13'49"S 147°53'12"E), 650 m, 18.i.2005, R. Mesibov, QVM 23:45893.

Paratypes. Male, Rattler Hill, EQ744353 (41°13'48"S 147°53'15"E), 650 m, 6.ix.1990, QVM 23:15466, dissected; female, Rattler Hill, EQ744353 (41°13'48"S 147°53'15"E), 650 m, 7.ix.1990, QVM

23:15468; female, Rattler Hill, EQ744353 (41°13'48"S 147°53'15"E), 650 m, 8.ix.1990, QVM 23:15467; male, Ben Nevis, EQ538147 (41°25'02"S 147°38'37"E), 890m, 15.iii.1993, QVM 23:15465, dissected; male, Caldbeck Creek, EQ471205 (41°21'55"S 147°33'47"E), 850 m, 26.xii.1994, R. Mesibov & T. Moule, AM KS91184 (formerly QVM 23:17758).

**Description.** Male c. 11 mm long,  $H = 1.2$  mm. In alcohol, under low magnification very pale brown in body colour with darker brown speckling in narrow transverse band posteriorly on metatergites. Antennae short, clavate (Fig. 69plo), about 1.75 $\times$  a socket diameter apart. Paranota reduced,  $R = 1.4$  (Fig. 70plo), posterior corners not turned up. Legs robust, tarsus longer than femur, tibia with prominent ventral distal swelling (Fig. 71plo). Epiproct with prominent paired, bluntly rounded projections. Telopodite (Fig. 64) widest near solenomere origin, reaching just past leg 6 when retracted. Solenomere arising at one-third the telopodite height, directed posterodistally at a small angle to telopodite axis, curving gradually laterally, terminating with small subapical projection at about one-quarter the prefemoral process height. Tibiotarsus roughly parallel to solenomere and about as wide but shorter, rod-like and pointed. Femoral process arising at level of solenomere origin, blade-like, forked at just over half its length; anterior branch basally pressed close to prefemoral process, directed distally, pointed and terminating at one-third to half the prefemoral process height (distal to solenomere tip); posterior branch short, wide, pointed, arising from anterior branch at right angle. **Prefemoral process at origin nearly as wide as telopodite base, slightly sinuous in anterior view, curving gradually posteriorly from about half its height, the distal third with a few very long, straight teeth on mesal edge directed basally and posterobasally and on lateral edge postero-basally.** Uncus prominent, deeply notched distally, arising from mesal side of prefemoral process at one-quarter to one-third the process height (distal to solenomere tip).

**Distribution and habitat.** Known from wet forest at three localities above 600 m in north-east Tasmania; the maximum distance between the localities is c. 30 km (Fig. 76). The *L. plomleyi* range has been carefully searched for millipedes and this species appears to be genuinely rare.

**Etymology.** In honour of Brian Plomley (1912-1994), Tasmanian scientist and scholar who encouraged biological research in north-east Tasmania.

### *Lissodesmus tarrabulga* sp. nov.

Figures 65, 66, 69tar, 70tar, 71tar, 78 (map)

**Material examined.** Holotype. Male, Australia, Victoria, North-east of Balook, 38°24'52"S 146°34'15"E, 620 m, 22.xii.2004, R. Mesibov, NMV K-9636.

Paratypes. Male, Jeeralang West Road, 0.1 km N of Binns Hill Junction, 38°26'30"S 146°29'E, pitfall emptied 10.i.1996, G. Milledge, ex sample NOH-2303, NMV K-9631; male, same details but pitfall emptied 5.iii.1996, ex sample NOH-2304, NMV K-9632; 3 males, W of Balook, 38°26'25"S 146°31'00"E, 600 m, 29.ix.2004, R. Mesibov & T. Moule, NMV K-9633 to K-9635, 2 dissected; 2 males, details as for holotype, AM KS91185; male, details as for holotype, anterior segments only, NMV K-9637.

**Description.** Male c. 17 mm long,  $H = 1.4$  mm. In alcohol, well-coloured specimens under low magnification pale brown in body colour with dispersed brown speckling on metatergites. Antennae moderately long (Fig. 69tar), about 1.75 $\times$  a socket diameter apart. Paranota wide,  $R = 1.6$ , lateral edge parallel to body axis, 2-3 inconspicuous posterior marginal teeth (Fig. 70tar), posterior corners not turned up. Legs robust, tarsus considerably longer than femur, tibia with prominent ventral distal swelling (Fig. 71tar). Telopodite (Figs 65, 66) reaching leg 6 when retracted. **Solenomere arising at half the telopodite height, directed distally, terminating at just over half the prefemoral process height, a rod-like, apically toothed, anteriorly directed projection arising at half the solenomere length on its anterior surface.** Tibiotarsus rod-like, pointed, directed posterodistally at small angle to telopodite axis, narrower than solenomere and about half as long. Femoral process arising at level of solenomere origin, blade-like, tapering, bluntly pointed, directed distally, not pressed close to prefemoral process, terminating at almost three-quarters the prefemoral process height (just distal to solenomere tip). **Prefemoral process at origin about half as wide as telopodite base, tapering strongly distally with simply pointed tip curving posteriorly.** Uncus prominent, arising on mesal side of prefemoral process at just over half the process height (just proximal to solenomere tip).

**Distribution and habitat.** Known from wet eucalypt forest at three sites over a 10 km section of the Strzelecki Ranges near Balook, in Gippsland (Fig. 78).

**Etymology.** Named for Tarra-Bulga National Park, the apparent centre of the small known range of this species.

*Tasmanopeltis* gen. nov.

**Type species.** *Tasmanopeltis grandis*, by present designation.

**Diagnosis.** Larger dalodesmids (30–35 mm long, 3.3 mm vertical diameter in type species) with head + 20 segments, normal pore formula, well-developed paranota with long posterior corner seta, hair-like structures arising from spiracles, spiracles on diplosegments juxtaposed over anterior leg. Telopodite straight, with small mesal solenomere and tibiotarsus, small lateral femoral process and large central prefemoral process. All processes arising at more than half the telopodite height; solenomere arising at almost two-thirds the telopodite height. Prefemoral process tip divided subapically into erect lateral branch with comb of long, mainly posterobasally directed teeth, and shorter, erect mesal branch with short, blunt, distally directed teeth.

**Distribution.** As for *T. grandis* sp. nov.

**Etymology.** A variation of *Australopeltis* Johns, 1964, which Johns probably derived from Latin *pelta* ("shield"); masculine.

**Remarks.** *Tasmanopeltis* is distinguished from *Lissodesmus* by its unusually large size (nearly two and a half times the calculated body volume of the next largest species, *L. montanus*, and more than 10 times that of the type, *L. modestus*); spiracles close together and with hair-like structures; process origins more than halfway along the telopodite; and a large, distal

projection on the prefemoral process, mesal to the latter's comb-like tip.

*Tasmanopeltis grandis* sp. nov.

Figures 5B, 67, 68, 69gra, 70gra, 71gra, 75 (map)

*Lissodesmus* sp. NE1.—Mesibov, 1994: 134.—Mesibov, 1996: 17.—Mesibov, 1997: 567.—Mesibov, 1998: 155.

**Material examined.** Holotype. Male, Australia, Tasmania. Speck Creek, EQ557542 (41°03'41"S 147°39'46"E), 330 m, 18.iii.1993, R. Mesibov, QVM 23:15555.

Paratypes. Male, Tin Hut Creek, EQ930505 (41°05'28"S 148°06'26"E), 140 m, 19.i.1989, R. Bashford, QVM 23:40767, pitfall; male, Eagle Hill, EQ550581 (41°01'34"S 147°39'15"E), 170 m, 10.iii.1993, R. Mesibov, AM KS91186 (ex QVM 23:15567); male, same details, QVM 23:15567; female, Speck Creek, EQ558537 (41°03'57"S 147°39'50"E), 150 m, 10.iii.1993, R. Mesibov, QVM 23:15598; male, Speck Creek, EQ576538 (41°03'53"S 147°41'07"E), 230 m, 10.iii.1993, R. Mesibov, QVM 23:15554, dissected; male, Mt Horror, EQ604547 (41°03'23"S 147°43'07"E), 220 m, 18.iii.1993, R. Mesibov, QVM 23:15557, dissected; male, Mt Horror, EQ588513 (41°05'14"S 147°42'00"E), 200 m, 24.iv.1993, R. Mesibov, QVM 23:15558; male, Mt Dismal area, EQ072330 (41°15'15"S 147°05'09"E), 320 m, 20.i.1995, R. Mesibov, QVM 23:17762; male, Ben Lomond, EQ483057 (41°29'55"S 147°34'43"E), 720 m, 16.vi.1995, R. Mesibov, QVM 23:21516.

Other material. 41 males, 49 females and 90 juveniles from Ansons River, "Aplico" property, Arnon River, Back Creek, Barrow Creek, Bell Creek, Ben Lomond, Ben Nevis, Blacksnake Marsh, Brady Kayes Lookout, Branhholm, Burns Creek, Caldbeck Creek, Carneys Creek, Chinaman Corner, Constance Creek, Duncraggen Hill, Eagle Hill, Foons Hill, Friend Creek, Glennons Road, Great Forester River, Harrys Hill, Hogarth Rivulet, Ikes Creek, Jewells Creek, Joseph Creek, Kamona, Martins Hill, Monazite Creek, Morris Ridge, Mother Logans Creek, Mt Arthur, Mt Cameron, Mt Dismal, Mt Horror, Mt Stronach, Musselboro, North Esk River, Northallerton Valley, Nunamara, Ockerbys Hills, Oxberry Creek, Patersonia, Pearly Brook, Rattler Hill, Scottsdale Mine, Sideling Range, Simons Road, Speck Creek, Spurs Rivulet, Swanee Creek, Telita, Tin Hut Creek, Traills Point, Weavers Creek, Wild Pig Hill, Williams Creek, Williams Hill and Wyena (see "*Lissodesmus* supplement" for details).

**Description.** Male c. 32 mm long,  $H = 3.3$  mm. In alcohol, well-coloured specimens red- to purple-brown dorsally, pale yellow-orange laterally, ventrally and on legs; at low magnification with fairly uniform red- to purple-brown colouring on metazonite, pale yellow-orange on paranotal and posterior metazonal margins, somewhat darker red- to purple brown on head and prozonites, legs darker dorsally, distal podomeres and antennae pale red. Antennae (Fig. 69gra) moderately long, slender, separated by about  $2\times$  socket diameter, sockets not deeply impressed; antennomere 6 widest, antennomere lengths typically decreasing in order 2, 3, 6, (4,5). Head with clypeus and frons densely setose, vertex bare; vertical sulcus extending to point about  $1.5\times$  socket diameter from line joining socket centres. Collum from above slightly wider than head, with nearly straight anterior border, steeply sloping shoulders, rounded posterior corners, slightly convex posterior margin with emarginate centre; posterior corner setae present and a few long setae in transverse line behind anterior margin and centrally; collum corners slightly ventral to paranotal margin of

segment 2. Paranota (Fig. 70gra) increasing in width from segment 2 to 5, fairly uniform in width posteriorly to segment 16, narrowing thereafter; paranota wide,  $R = 1.8$  on segment 12; lateral margins more convex and posterior corners more produced posteriorly, on most segments the paranota widest anteriorly; lateral margins with 3-4 notches, typically each with short seta, the most anterior notch with longest seta, sometimes as long as posterior corner seta, the latter arising on most segments on mesal side of projecting posterior corner, close to base of latter; the margins straight in lateral view but inclined upwards posteriorly at c.  $15^\circ$  to horizontal. Segment surfaces smooth, metatergites bare apart from short, sparse setae in 2-3 transverse rows anteriorly. Pore formula 5, 7, 9, 10, 12, 13, 15-19; ozopore opening dorsolaterally on paranotum at about three-quarters the distance from anterior to posterior paranotal margins, close to lateral margin. Spiracles (Fig. 5B) enlarged, on diplosegments the posterior spiracle almost touching anterior spiracle over anterior leg, rims very thin, projecting, all spiracles with dense mass of emergent hair-like structures. Sternite tetrads longer than wide, transverse furrow deep, longitudinal furrow less deep. Legs (Fig. 71gra) variably swollen from segment 3 posteriorly, mostly with strongly arched prefemur, slightly arched femur, slight ventral distal swellings on postfemur and tibia; tarsus slightly curved; podomere lengths decreasing in order tarsus, femur, prefemur, (postfemur, tibia); dense "brush" setae on prefemur, femur, postfemur; sphaerotrichomes on all five podomeres on legs near gonopods; leg 2 coxa with genital opening on mesodistal swelling, only slightly raised above coxal surface; paired coxae of legs 6 and 7 well separated, slightly separated on legs 5, not separated on legs 4. Gonopod aperture about one-third as wide as segment 7 prozonite, more or less rectangular (wider than long) with rounded corners in ventral view, in lateral view with lateral margin strongly produced posteriorly. Gonopod coxae entirely contained within aperture, fairly small, more or less ellipsoid, lightly joined along midline distally, with dense, short setae on ventromesal surface distally; cannulae prominent. Telopodites (Figs 67, 68) separate, straight, lightly setose posteriorly from base to level of solenomere origin, reaching leg 5 when retracted. **Solenomere arising from anteromesal surface of telopodite at almost two-thirds the telopodite height, directed posterodistally at somewhat less than  $45^\circ$  to telopodite axis, curving very slightly laterally, tapering gradually, tip curving distally, no subapical projection or similar structure, terminating at about four-fifths the telopodite height (about two-thirds the prefemoral process height).** Tibiotarsus arising a little posterior and distal to solenomere and more or less parallel to it, rod-like, bluntly pointed, about one-third the solenomere length. Femoral process arising just proximal to solenomere origin on antero-lateral surface, mesolaterally flattened, pressed close near origin to prefemoral process, widening distally with truncate, sinuous, inconspicuously toothed distal edge, terminating at just over half the prefemoral process height (proximal to solenomere tip). **Prefemoral process at origin about half as wide as telopodite base, widening distally and dividing at about half its height into well-separated lateral and mesal branches; lateral branch curving posteriorly with a comb of**

**10–15 long, straight, mainly posterobasally directed teeth on mesal edge; mesal branch one-third to one-half the height of lateral branch (terminating just distal to solenomere tip), bluntly pointed with mesal surface armed with 3–4 short, blunt, posterodistally directed teeth.** Uncus a large posterior extension of mesal edge of prefemoral process just proximal to solenomere tip, widely notched on outer edge. Hypoproct paraboloid in outline; preanal ring with numerous long setae; epiproct projecting well past anal valves, in dorsal outline triangular with truncated apex. Female slightly larger than male, c. 35 mm long, legs thinner, otherwise with same coloration, paranotal form and spiracle features. Posterior rim of epigynal opening strongly produced, with rounded corners and elevated central portion; cyphopods not examined.

**Distribution and habitat.** In dry and wet eucalypt forest and cool temperate rainforest over c. 3500 km<sup>2</sup> in north-east Tasmania (Fig. 75), from Mt Dismal in the Tamar Valley east to Ansons River, from Gladstone south to Ben Lomond, and from near sea level to 920 m. The western range boundary of *T. grandis* lies within the biogeographical divide known as the East Tamar Break (Mesibov, 1994), and is particularly sharp near Weavers Creek (Mesibov, 1997). Adults of *T. grandis* are generally found in or under rotting logs and only rarely burrow into the soil.

**Etymology.** Latin *grandis* ("large, magnificent"), adjective.

**Remarks.** Although *T. grandis* is the largest polydesmidan in Tasmania, it is remarkably cryptic in its habits, and the first known museum specimen was collected less than 20 years ago (on Mt Arthur in 1987).

## Acknowledgements

This study was supported by a grant from the Plomley Foundation. I thank David Steele (University of Tasmania) for acquiring the SEM images; Gonzalo Giribet (Harvard University) for access to the *Lissodesmus modestus* types; Peter Lillywhite (Museum Victoria) for the loan of specimens; Genefer Walker-Smith (Tasmanian Museum and Art Gallery) and Cathy Young (Department of Primary Industries, Water and Environment, Tasmania) for advice on millipede holdings; Dennis Black (La Trobe University) for the opportunity to examine the Lower Gordon River Scientific Survey material held in the Australian National Insect Collection; and Mark Harvey (Western Australian Museum) for alerting me to his collection of *L. milledgei*. I am grateful to Geoff and Jackie Tims for inviting me to collect on "Lapoinya", near Yarragon, and to other Gippsland landowners who allowed me access to their properties. I am especially grateful to my wife, Trina Moule, for her able assistance in the field over many years. A draft of this paper was greatly improved by comments from Mark Harvey and Gary Poore.

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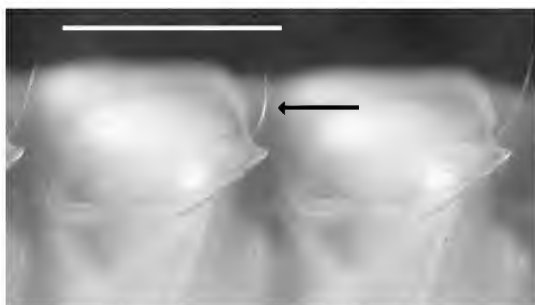


Figure 1. *Lissodesmus perporosus* Jeekel, 1984, male. Left lateral view of midbody paranotum, showing posterior corner seta (arrow). Scale bar = 1.0 mm.

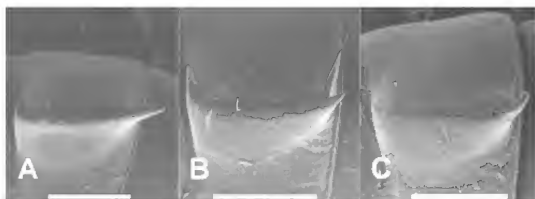


Figure 4. (A) *L. modestus* Chamberlin, 1920, male from Edwards Road, Huon River, ex QVM 23:15294; (B) *L. hamatus* sp. nov., male paratype ex QVM 23:16073; (C) *L. anas* sp. nov., male paratype ex QVM 23:17657. Left lateral SEM views of midbody segment, showing nearly straight paranotal margin (A), slightly upturned posterior corner (B) and strongly upturned posterior corner (C). Scale bars = 0.5 mm.

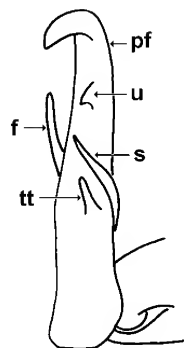


Figure 2. Diagrammatic posteromesal view of the right gonopod telopodite of a member of the *Lissodesmus* group. f = femoral process, pf = prefemoral process, s = solenomere, tt = tibiotarsus, u = uncus.

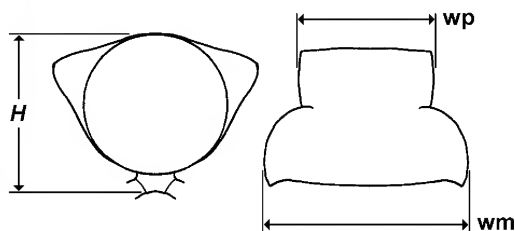


Figure 3. Diagrammatic posterior (left) and dorsal (right) views of a polydesmidan midbody segment, showing measurement limits for height  $H$ , prozonite width  $w_p$  and paranotal width  $w_m$ . Relative paranotal width  $R = w_m/w_p$ .

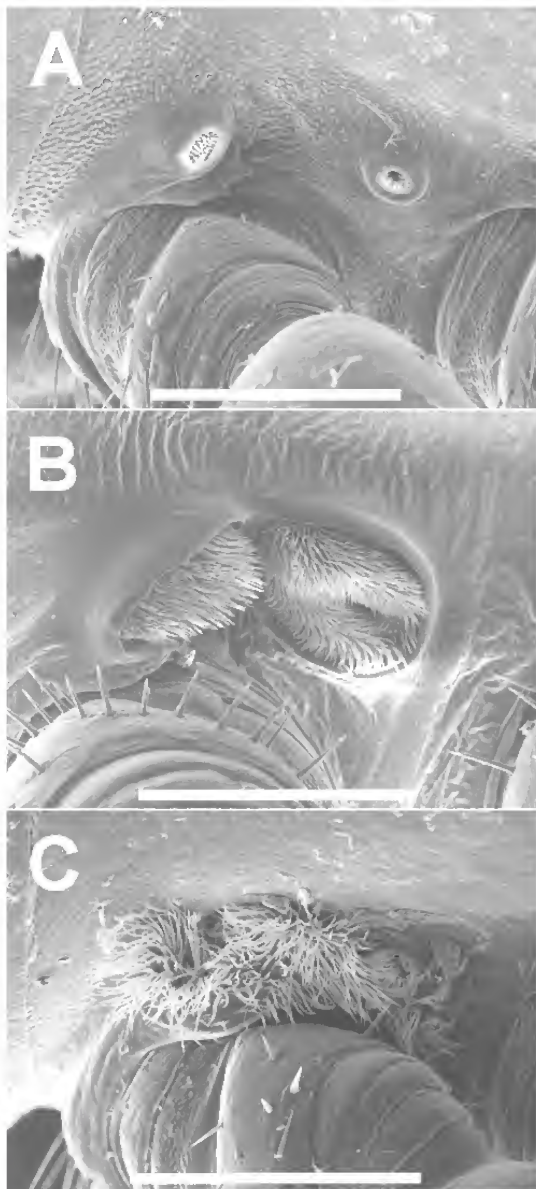


Figure 5. (A) *L. modestus* Chamberlin, 1920, male from Edwards Road, Huon River, ex QVM 23:15294; (B) *Tasmanopeltis grandis* gen. et sp. nov., male paratype, QVM 23:15554; (C) *L. anas* sp. nov., male paratype ex QVM 23:17657. Left lateral SEM views of midbody segment, showing spiracles. Scale bars = 0.25 mm (A, C) and 0.35 mm (B).

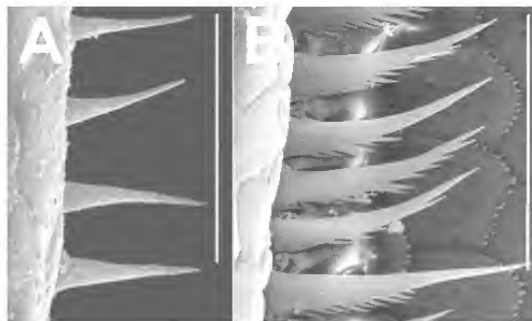


Figure 6. (A) *L. latus* sp. nov., male paratype ex QVM 23:17490, (B) *L. hamatus* sp. nov., male paratype ex QVM 23:16073. SEM views of a group of limbus elements on a midbody segment. Scale bars = 0.025 mm; anterior is to the left.

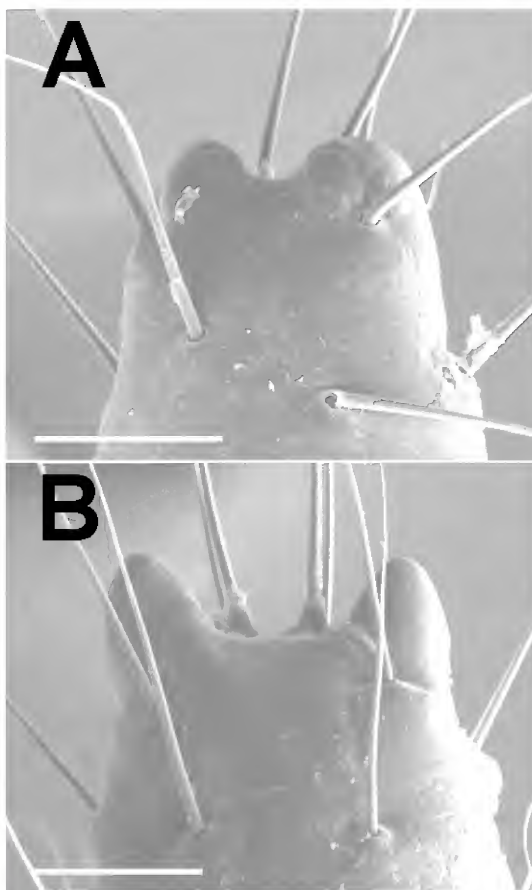


Figure 7. (A) *L. modestus* Chamberlin, 1920, male from Edwards Road, Huon River, ex QVM 23:15294; (B) *L. adrianae* Jeekel, 1984, male ex QVM 23:21220. Dorsal SEM views of epiproct. Scale bars = 0.1 mm.

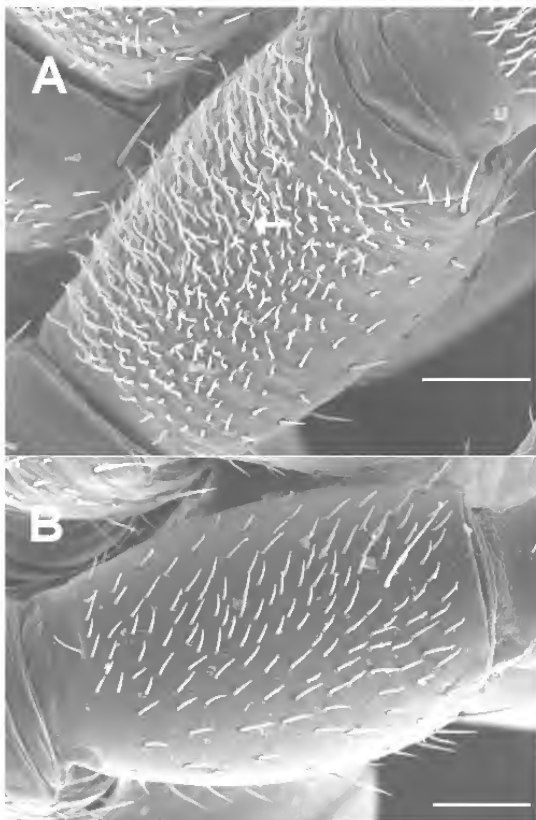


Figure 8. (A) *L. modestus* Chamberlin, 1920, male from Edwards Road, Huon River, ex QVM 23:15294; (B) *L. orarius* sp. nov., male paratype ex QVM 23:17683. Ventral SEM views of leg 6 prefemur in situ. Arrow points to one of seven sphaerotrichomes visible among "brush" setae on *L. modestus* prefemur; sphaerotrichomes are lacking on *L. orarius* prefemur. Scale bars = 0.1 mm.



Figure 10. *L. perporosus* Jeekel, 1984, males from Wombat Hill, W of Waratah. SEM views of paranotal margin of midbody segment. (A) stadium 5, ex QVM 23:17291; (B) stadium 6, ex QVM 23:17291; (C) stadium 7, ex QVM 23:17291; (D) stadium 8, ex QVM 23:17429. Scale bars = 0.25 mm.

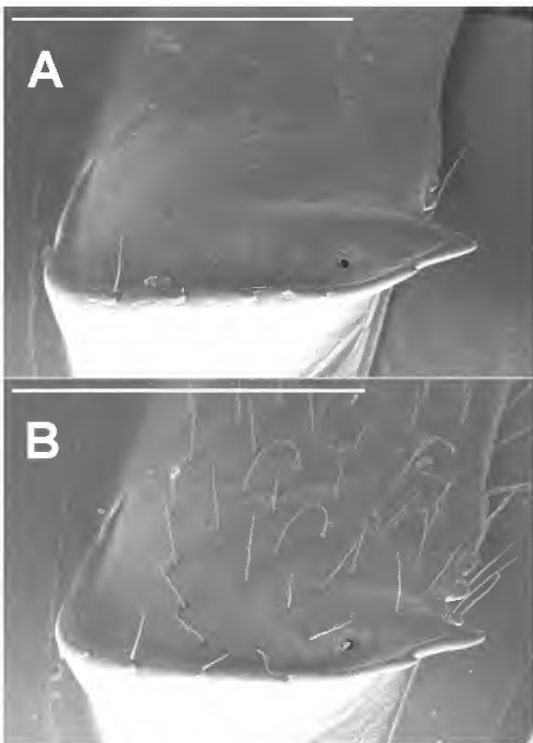


Figure 9. *L. latus* sp. nov., females. Left dorsolateral SEM views of midbody segment of typical form (A) from Sterling River, QVM 23:17525, and furry form (B) from S of Mt Cripps, ex QVM 23:17516.



Figure 11. *L. adrianae* Jeekel, 1984, male from Ben Lomond, ex QVM 23:21220. SEM view of gonopods in situ. Scale bar = 0.5 mm.

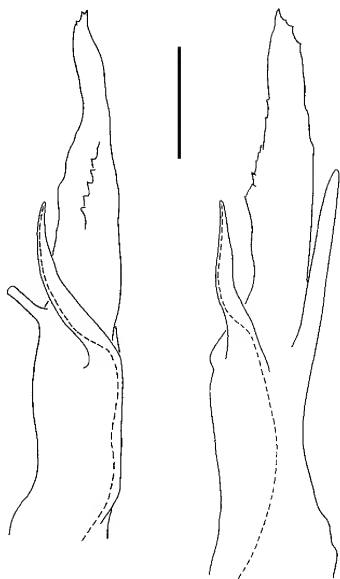


Figure 12. *L. adrianae* Jeekel, 1984, male from Ben Lomond, ex QVM 23:21220. Mesal (left) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.

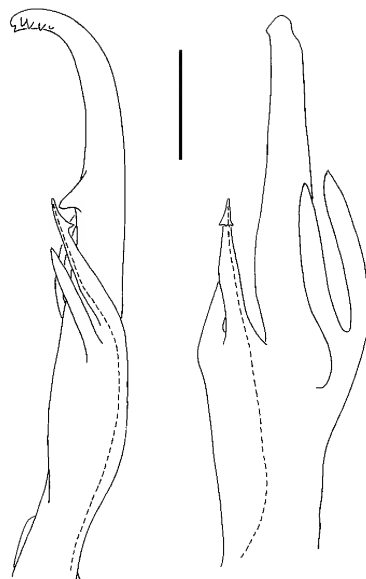


Figure 13. *L. alisonae* Jeekel, 1984, male from Franklin Village, ex QVM 23:15440. Mesal (left) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.

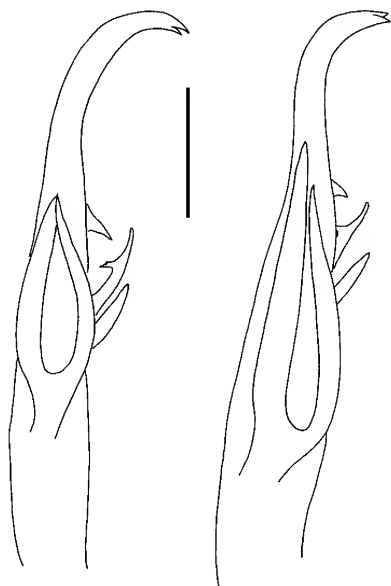


Figure 14. *L. alisonae* Jeekel, 1984, males from Franklin Village near Launceston (left), ex QVM 23:15440, and "Bowood" property near Bridport (right), ex QVM 23:15442. Lateral views of right gonopod telopodite. Scale bar = 0.25 mm.



Figure 15. *L. anas* sp. nov., male paratype ex QVM 23:17657. SEM view of gonopods in situ. Scale bar = 0.5 mm.



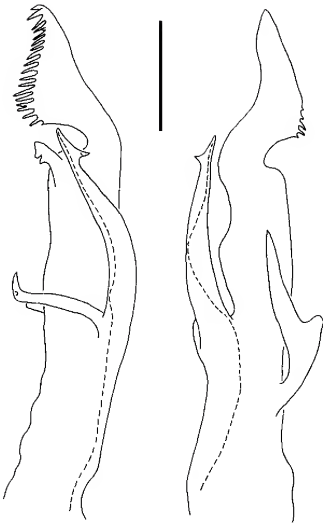


Figure 16. *L. anas* sp. nov., male paratype ex QVM 23:40749. Mesal (left) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.



Figure 17. *L. bashfordi* sp. nov., male paratype ex QVM 23:45946. SEM view of gonopods in situ. Scale bar = 0.5 mm.

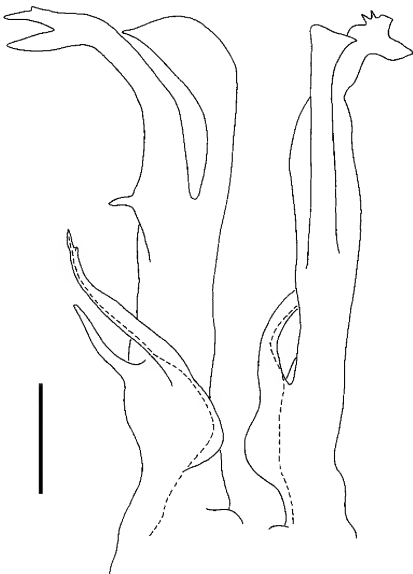


Figure 18. *L. bashfordi* sp. nov., male paratype ex QVM 23:45946. Mesal (left) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.



Figure 19. *L. blackwoodensis* sp. nov., male paratype, NMV K-8923. SEM view of gonopods in situ. Scale bar = 0.5 mm.

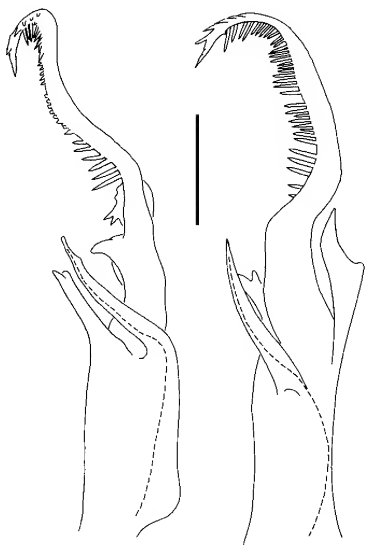


Figure 20. *L. blackwoodensis* sp. nov., male paratype, NMV K-8924. Mesal (left) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.

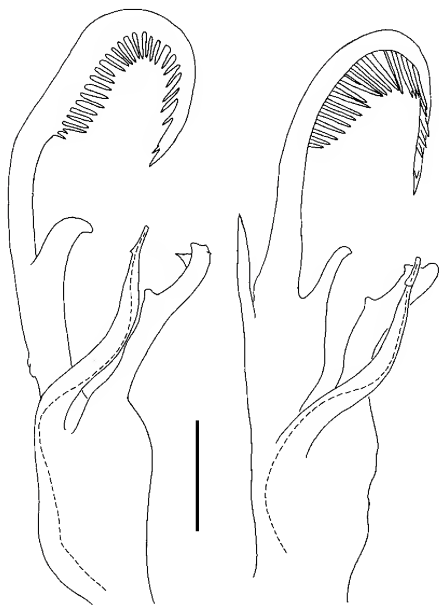


Figure 22. *L. catrionae* sp. nov., male paratype, NMV K-8971. Mesal (left) and anterior (right) views of left gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.



Figure 21. *L. catrionae* sp. nov., male paratype, NMV K-8970. SEM view of right gonopod in situ. Scale bar = 0.5 mm.



Figure 23. *L. clivulus* sp. nov., male paratype ex QVM 23:17667. SEM view of gonopods in situ. Scale bar = 0.5 mm.

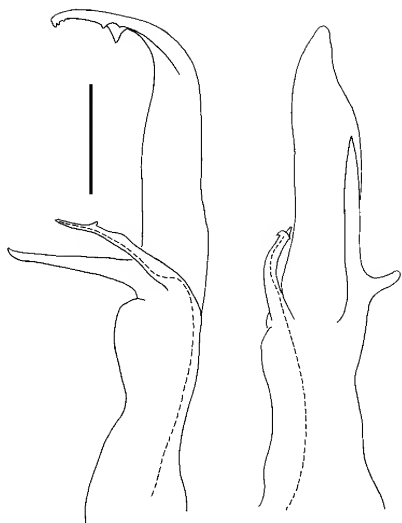


Figure 24. *L. clivulus* sp. nov., male paratype ex QVM 23:17667. Mesal (left) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.



Figure 25. *L. cognatus* sp. nov., male paratype ex QVM 23:15283. SEM view of gonopods in situ. Scale bar = 0.5 mm.

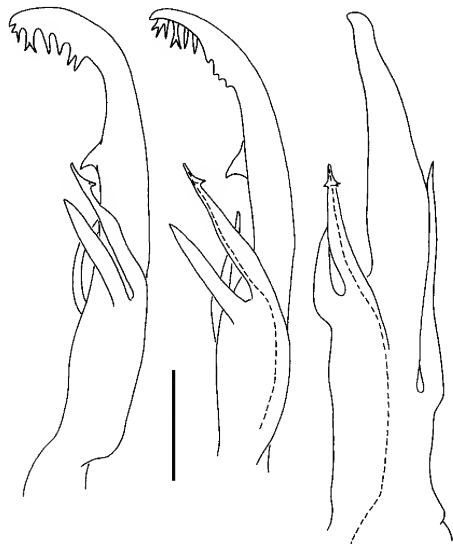


Figure 26. *L. cognatus* sp. nov., male paratypes from Coxs Creek in the eastern range patch (far left), ex QVM 23:24738, and Weavers Creek in the western range patch (centre and right), ex QVM 23:21562. Mesal (left and centre) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.

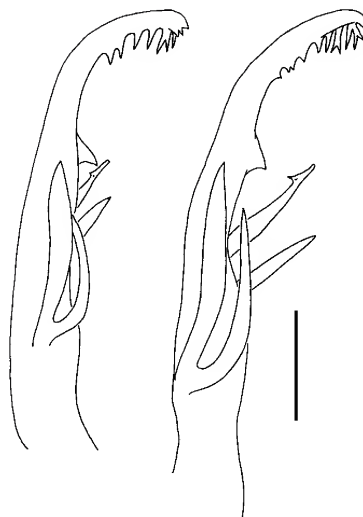


Figure 27. *L. cognatus* sp. nov., male paratypes from Coxs Creek in the eastern range patch (left), ex QVM 23:24738, and Weavers Creek in the western range patch (right), ex QVM 23:21562. Lateral views of right gonopod telopodite. Scale bar = 0.25 mm.



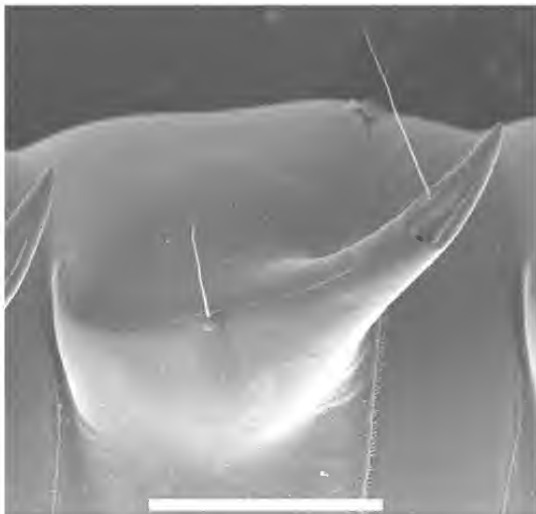


Figure 28. *L. cornutus* sp. nov., male paratype ex QVM 23:24824. Left lateral SEM view of midbody segment. Scale bar = 0.5 mm.

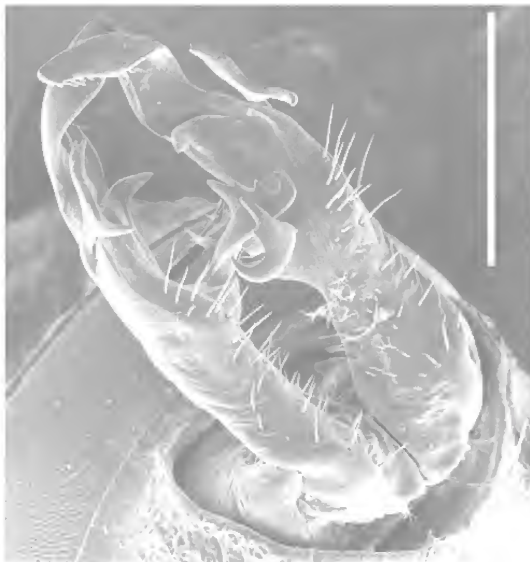


Figure 29. *L. cornutus* sp. nov., male paratype ex QVM 23:24824. SEM view of gonopods in situ. Scale bar = 0.5 mm.

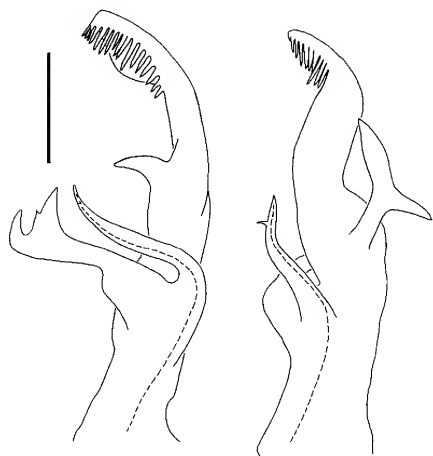


Figure 30. *L. cornutus* sp. nov., male paratype ex QVM 23:24824. Mesal (left) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.



Figure 31. *L. devexus* sp. nov., male paratype from Shepherds Rivulet, 6 km SE of the type locality, ex QVM 23:15509. SEM view of gonopods in situ. Scale bar = 0.5 mm.

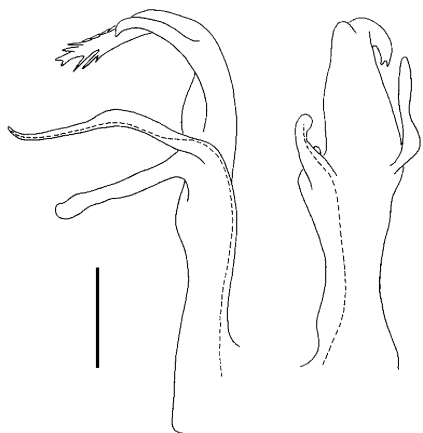


Figure 32. *L. devexus* sp. nov., male paratype ex QVM 23:15515. Mesal (left) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.

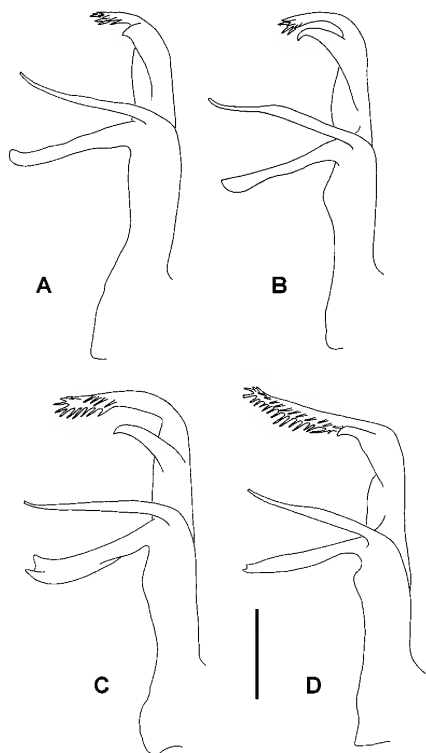


Figure 33. *L. devexus* sp. nov., male paratypes from (A) Retreat, ex QVM 23:21534, (B) Weldborough, QVM 23:15512, (C) Mt Roland, ex QVM 23:15506 and (D) Lowes Mount, QVM 23:21542. Mesal views of right gonopod telopodite. Scale bar = 0.25 mm.

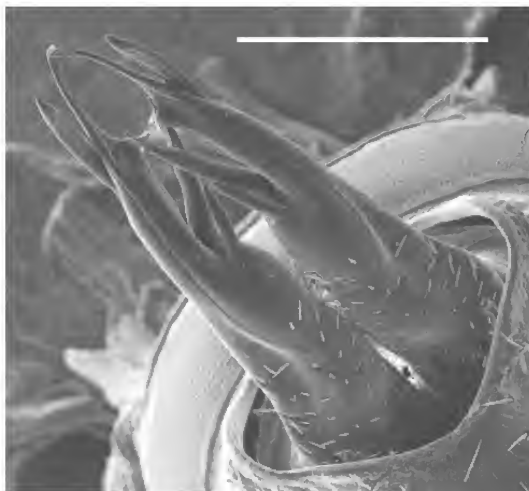


Figure 34. *L. dignomontis* sp. nov., male paratype, NMV K-9664. SEM view of gonopods in situ. Scale bar = 0.5 mm.

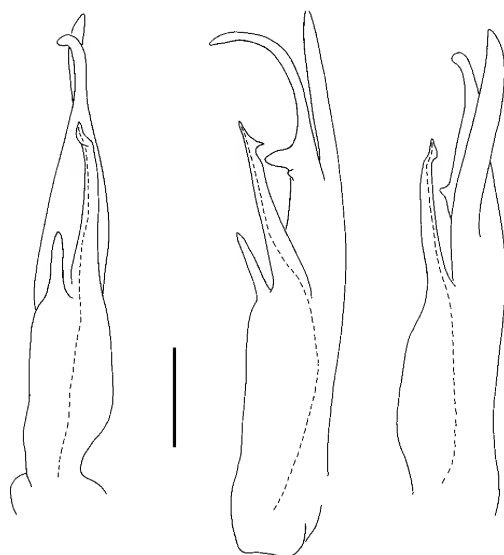


Figure 35. *L. dignomontis* sp. nov., male paratype, NMV K-9507. Posterior (left), mesal (centre) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.



Figure 36. *L. gippslandicus* sp. nov., male paratype, NMV K-9483. SEM view of gonopods in situ. Scale bar = 0.5 mm.

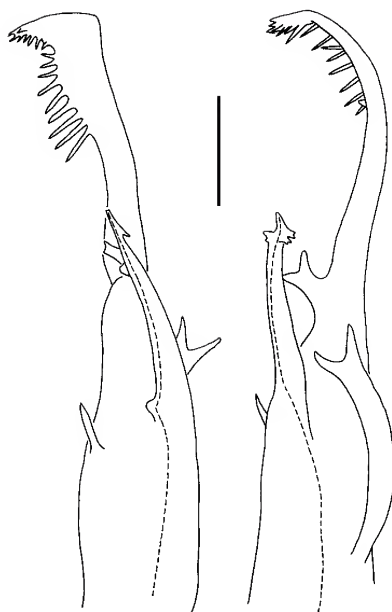


Figure 37. *L. gippslandicus* sp. nov., male paratype, NMV K-9484. Mesal (left) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.



Figure 38. *L. hamatus* sp. nov., male paratype ex QVM 23:16073. SEM view of gonopods in situ. Scale bar = 0.5 mm.

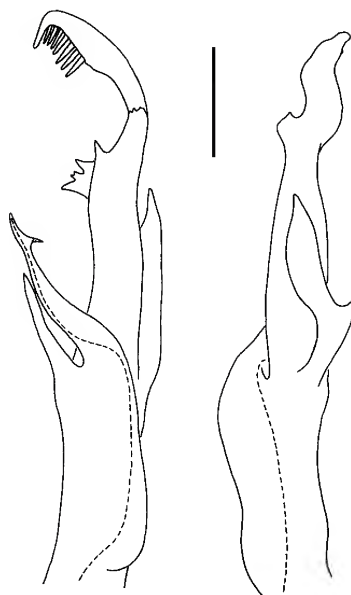


Figure 39. *L. hamatus* sp. nov., male paratype ex QVM 23:16073. Mesal (left) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.



Figure 40. *L. horridomontis* sp. nov., male paratype ex QVM 23:15490. SEM view of gonopods in situ. Scale bar = 0.5 mm.



Figure 42. *L. inopinatus* sp. nov., male paratype ex QVM 23:16164. SEM view of gonopods in situ. Scale bar = 0.5 mm.

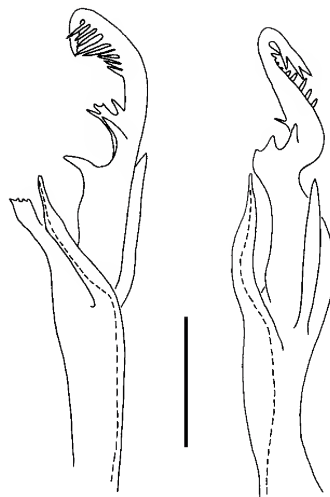


Figure 41. *L. horridomontis* sp. nov., male paratype ex QVM 23:15490. Mesal (left) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.

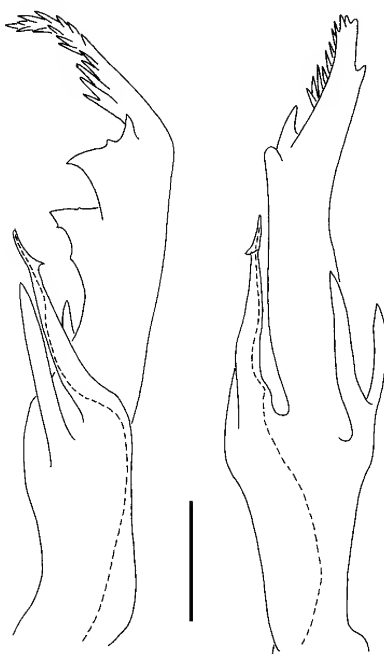


Figure 43. *L. inopinatus* sp. nov., male paratype ex QVM 23:16164. Mesal (left) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.



Figure 44. *L. johnsi* sp. nov., male paratype, NMV K-9683. SEM view of gonopods in situ. Scale bar = 0.5 mm.



Figure 47. *L. macedonensis* sp. nov., male paratype, NMV K-9511. SEM view of gonopods in situ. Scale bar = 0.5 mm.

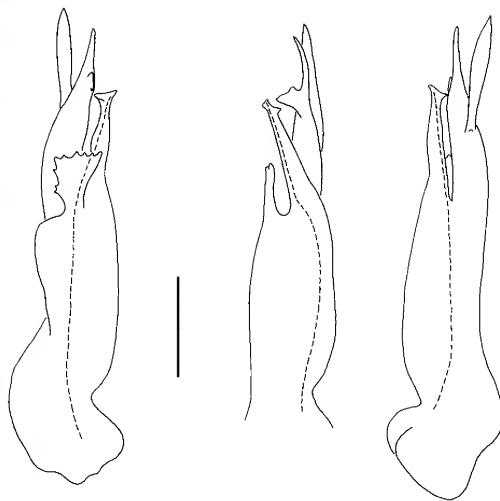


Figure 45. *L. johnsi* sp. nov., male paratype, NMV K-9506. Posterior (left), mesal (centre) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.

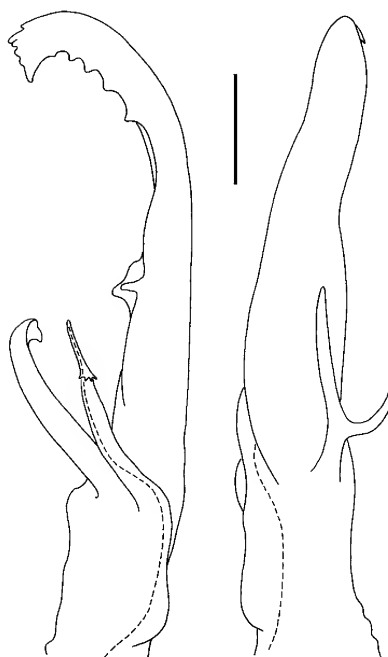


Figure 46. *L. latus* sp. nov., male paratype ex QVM 23:17490. Mesal (left) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.

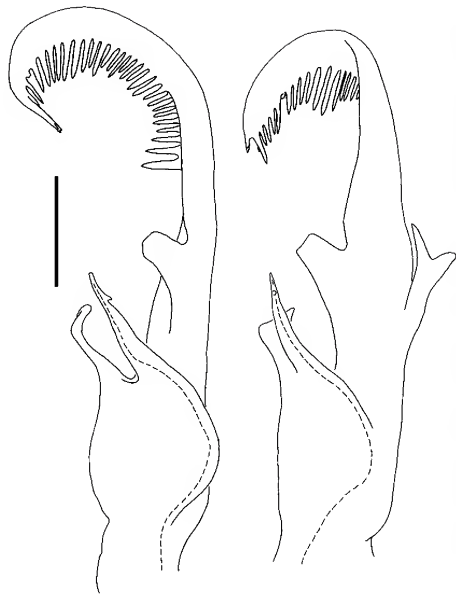


Figure 48. *L. macedonensis* sp. nov., male paratype, NMV K-9512. Mesal (left) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.



Figure 49. *L. martini* (Carl, 1902), male from Acheron Gap area, NMV K-9590. SEM view of gonopods in situ. Scale bar = 0.5 mm.

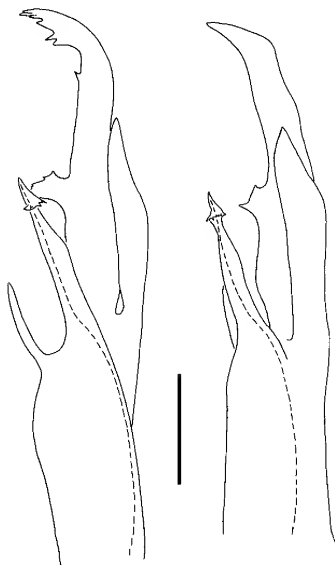


Figure 50. *L. martini* (Carl, 1902), male from Acheron Gap area, NMV K-9591. Mesal (left) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.

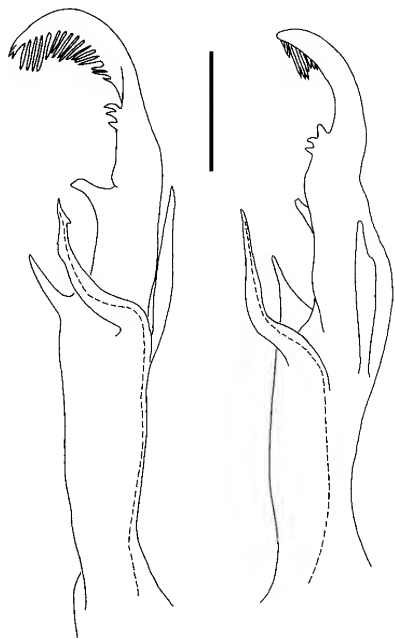


Figure 51. *L. milledgei* sp. nov., male paratype, NMV K-9606. Mesal (left) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.





Figure 52. *L. modestus* Chamberlin, 1920, male from Edwards Road, Huon River, ex QVM 23:15294. Posterior SEM view of gonopods in situ. Scale bar = 0.5 mm.



Figure 53. *L. modestus* Chamberlin, 1920, male from Edwards Road, Huon River, ex QVM 23:15294. Mesal view of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.



Figure 54. *L. montanus* sp. nov., male paratype, QVM 23:17716. SEM view of gonopods in situ. Scale bar = 0.5 mm.



Figure 55. *L. montanus* sp. nov., male paratype, QVM 23:17715. Mesal view of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.





Figure 56. *L. orarius* sp. nov., male paratype ex QVM 23:17683. SEM view of gonopods in situ. Scale bar = 0.5 mm.



Figure 58. *L. otwayensis* sp. nov., male paratype, NMV K-9620. SEM view of gonopods in situ. Scale bar = 0.5 mm.

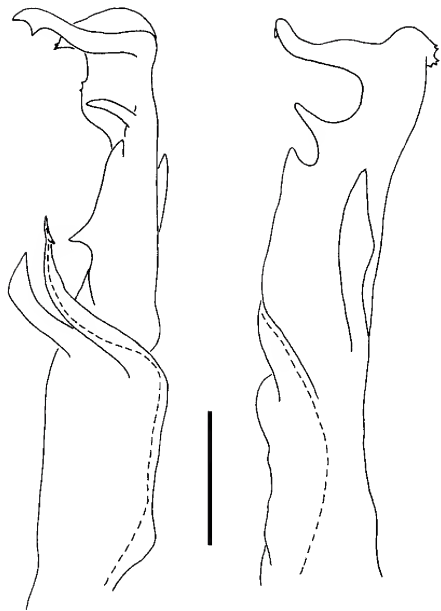


Figure 57. *L. orarius* sp. nov., male paratype ex QVM 23:17693. Mesal (left) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.

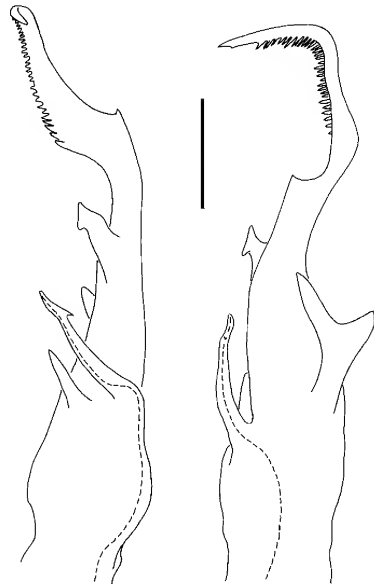


Figure 59. *L. otwayensis* sp. nov., male paratype, NMV K-9619. Mesal (left) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.

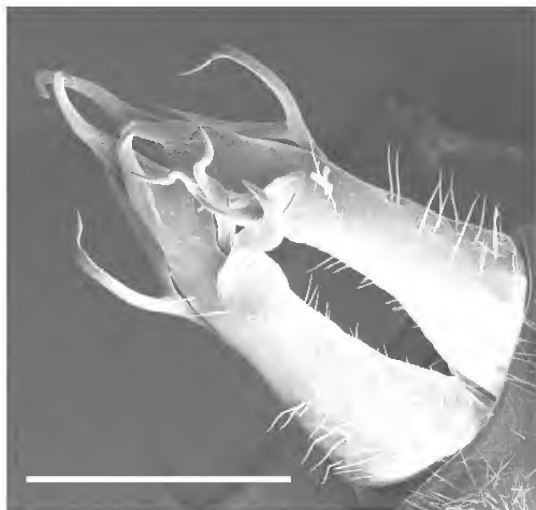


Figure 60. *L. peninsulensis* sp. nov., male paratype, QVM 23:16173. SEM view of gonopods in situ. Scale bar = 0.5 mm.



Figure 62. *L. perporosus* Jeekel, 1984, male from Wombat Hill, W of Waratah, ex QVM 23:17419. SEM view of right gonopod in situ. Scale bar = 0.5 mm.

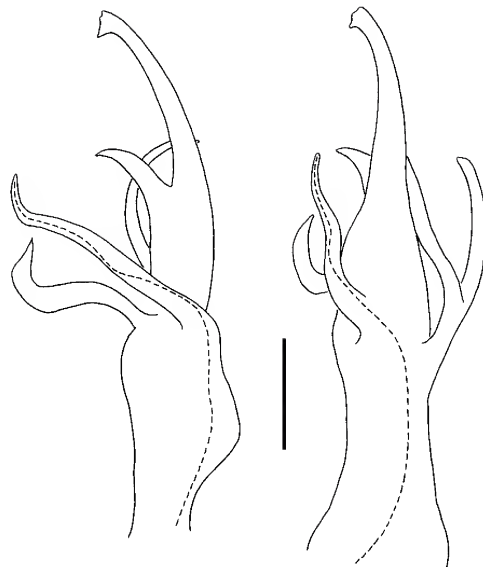


Figure 61. *L. peninsulensis* sp. nov., male paratype, QVM 23:16172. Mesal (left) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.

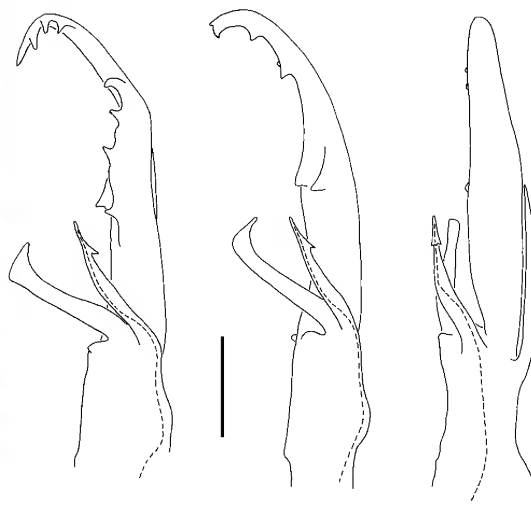


Figure 63. *L. perporosus* Jeekel, 1984, males from Wombat Hill, W of Waratah (centre and right), ex QVM 23:17419, and Maggs Mountain (left), QVM 23:17411. Mesal (left and centre) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.

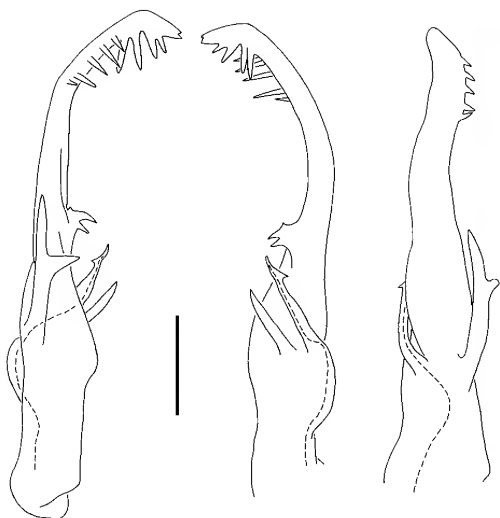


Figure 64. *L. plumleyi* sp. nov., male paratype, QVM 23:15465. Lateral (left), mesal (centre) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.

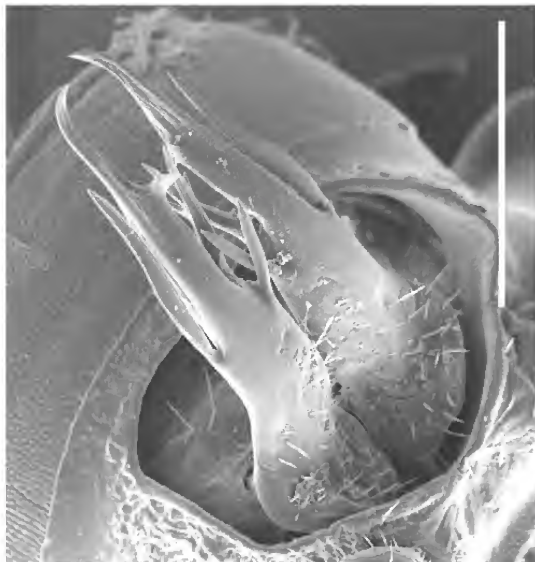


Figure 65. *L. tarrabulga* sp. nov., male paratype, NMV K-9634. SEM view of gonopods in situ. Scale bar = 0.5 mm.

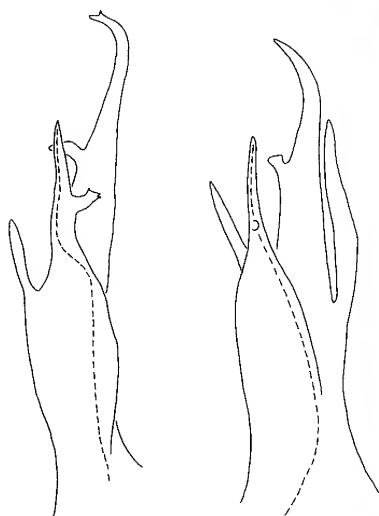


Figure 66. *L. tarrabulga* sp. nov., male paratype, NMV K-9635. Mesal (left) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.



Figure 67. *Tasmanopeltis grandis* gen. et sp. nov., male paratype, QVM 23:15554. SEM view of gonopods in situ. Scale bar = 1.0 mm.

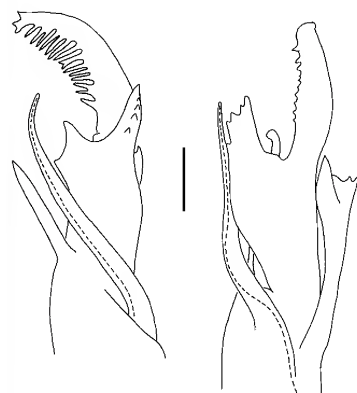


Figure 68. *Tasmanopeltis grandis* gen. et sp. nov., male paratype, QVM 23:15557. Mesal (left) and anterior (right) views of right gonopod telopodite. Dashed lines indicate course of prostatic groove; scale bar = 0.25 mm.

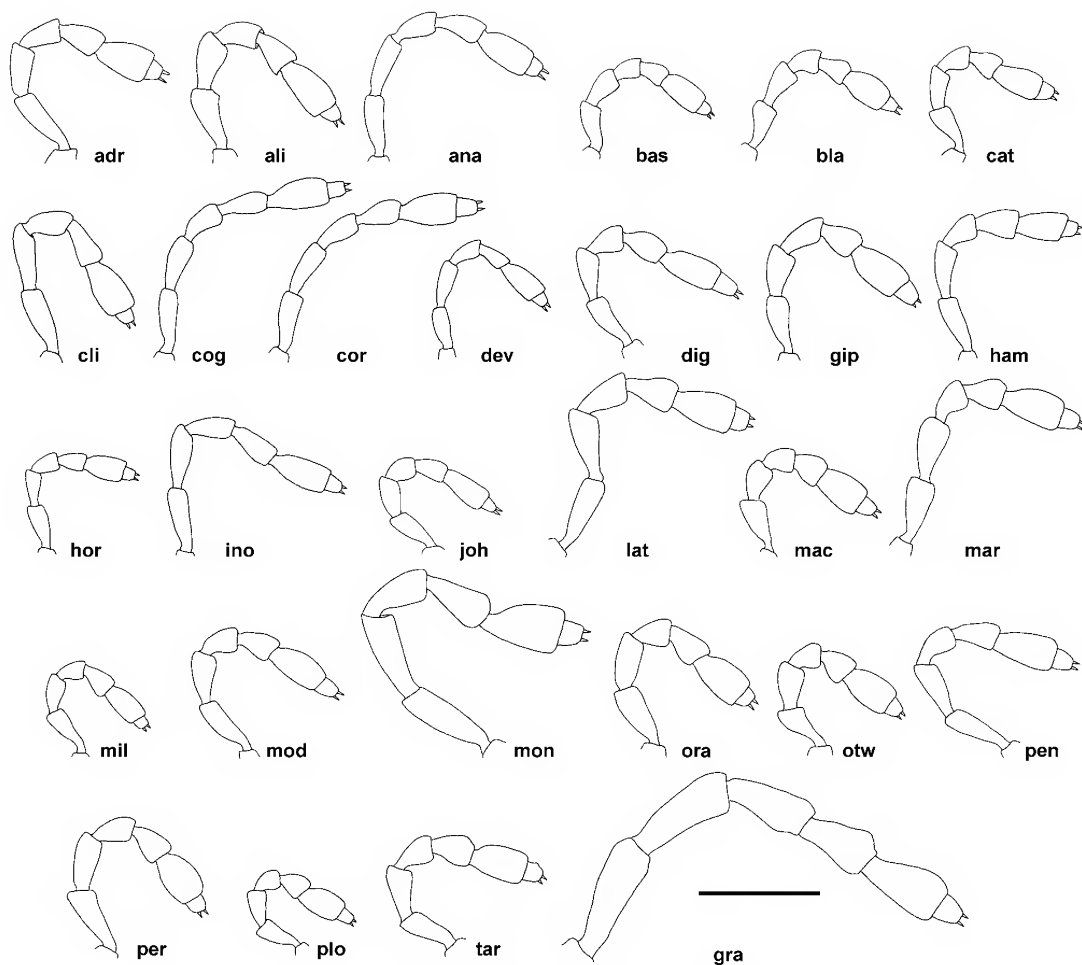


Figure 69. Male antennae of *Lissodesmus adrianae* Jeekel, 1984 (**adr**; ex QVM 23:21220), *L. alisonae* Jeekel, 1984 (**ali**; ex QVM 23:15440), *L. anas* sp. nov. (**ana**; paratype ex QVM 23:40749), *L. bashfordi* sp. nov. (**bas**; paratype ex QVM 23:45946), *L. blackwoodensis* sp. nov. (**bla**; paratype, NMV K-8924), *L. catrionae* sp. nov. (**cat**; paratype, NMV K-8971), *L. clivulus* sp. nov. (**cli**; paratype ex QVM 23:17667), *L. cognatus* sp. nov. (**cog**; paratype ex QVM 23:24738), *L. cornutus* sp. nov. (**cor**; paratype ex QVM 23:24824), *L. devexus* sp. nov. (**dev**; paratype ex QVM 23:15515), *L. dignomontis* sp. nov. (**dig**; paratype NMV-9507), *L. gippslandicus* sp. nov. (**gip**; paratype NMV K-9484), *L. hamatus* sp. nov. (**ham**; paratype ex QVM 23:16073), *L. horridomontis* sp. nov. (**hor**; paratype ex QVM 23:15490), *L. inopinatus* sp. nov. (**ino**; paratype ex QVM 23:16164), *L. johnsi* sp. nov. (**joh**; paratype NMV K-9683), *L. latus* sp. nov. (**lat**; paratype ex QVM 23:17490), *L. macedonensis* sp. nov. (**mac**; paratype NMV K-9512), *L. martini* (Carl, 1902) (**mar**; NMV K-9591), *L. milledgei* sp. nov. (**mil**; paratype NMV K-9606), *L. modestus* Chamberlin, 1920 (**mod**; ex QVM 23:15294), *L. montanus* sp. nov. (**mon**; paratype QVM 23:17716), *L. orarius* sp. nov. (**ora**; paratype ex QVM 23:17693), *L. otwayensis* sp. nov. (**otw**; paratype NMV K-9619), *L. peninsulensis* sp. nov. (**pen**; paratype QVM 23:16171), *L. perporosus* Jeekel, 1984 (**per**; paratype ex QVM 23:17419), *L. plomleyi* sp. nov. (**plo**; paratype QVM 23:15466), *L. tarabulga* sp. nov. (**tar**; NMV K-9635) and *Tasmanopeltis grandis* gen. et sp. nov. (**gra**; paratype QVM 23:15558). Scale bar = 1.0 mm.

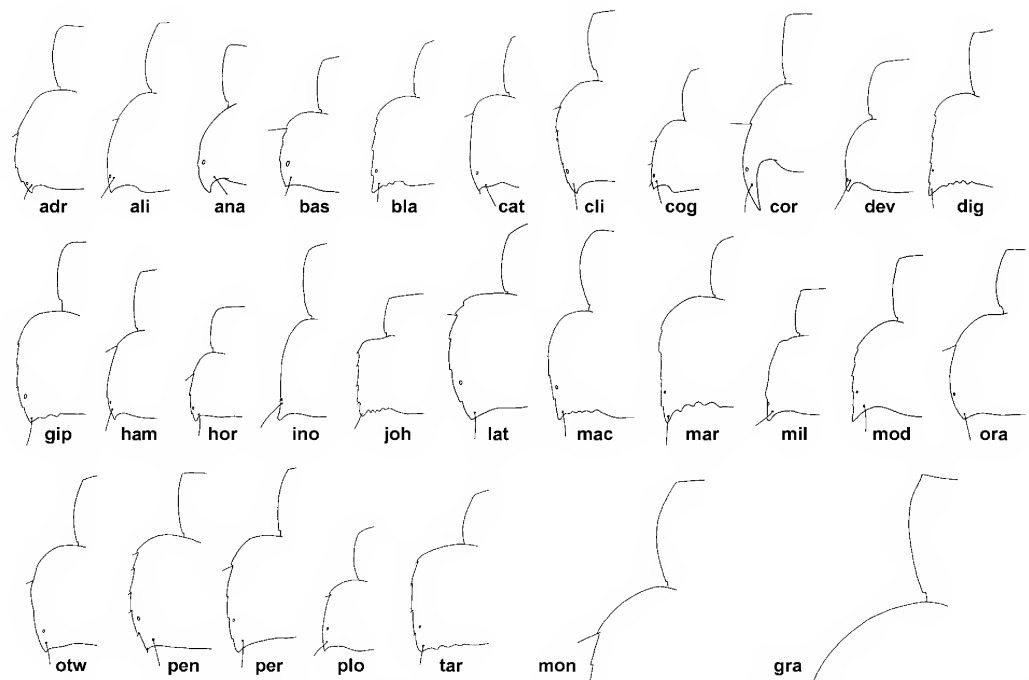


Figure 70. Left side dorsal profiles of segment 12 of male *Lissodesmus* spp. and *Tasmanopeltis grandis* gen. et sp. nov., and of segment 13 of male *L. plomleyi* sp. nov. Species codes and specimen details as in Fig. 65. The ozopore opening is shown as a small ellipse near the paranotal margin in all cases. Scale bar = 1.0 mm.

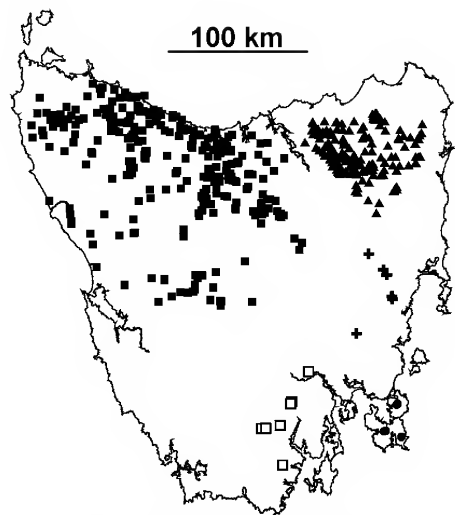


Figure 72. Localities in Tasmania of *Lissodesmus adrianae* (triangles), *L. bashfordi* sp. nov. (open squares), *L. inopinatus* sp. nov. (crosses), *L. peninsulensis* sp. nov. (dots) and *L. perporosus* (filled squares).

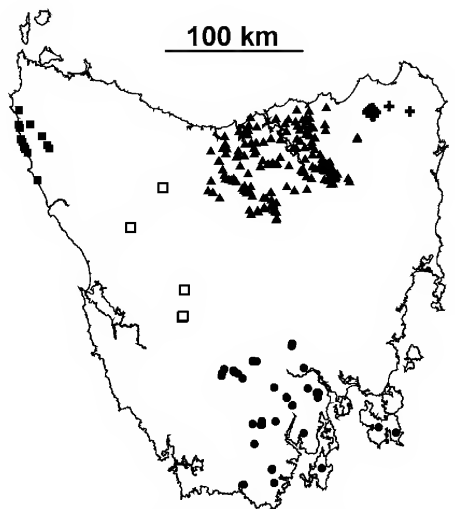


Figure 73. Localities in Tasmania of *Lissodesmus alisonae* (triangles), *L. clivulus* sp. nov. (filled squares), *L. horridomontis* sp. nov. (crosses), *L. modestus* (dots) and *L. montanus* sp. nov. (open squares).

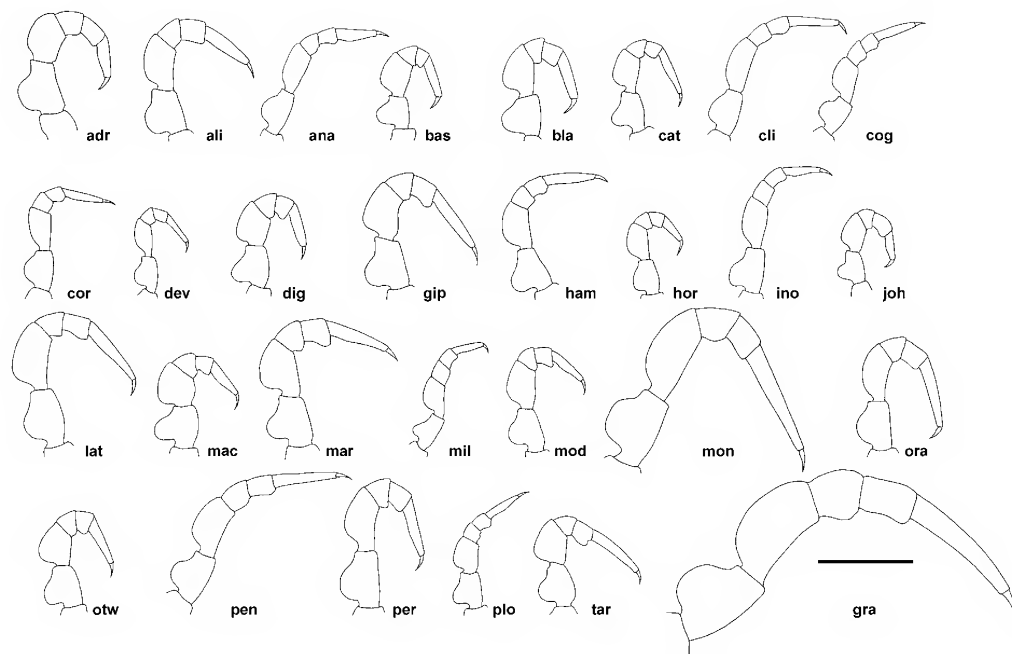


Figure 71. Male leg 7 of *Lissodesmus* spp. and *Tasmanopeltis grandis* gen. et sp. nov. Species codes and specimen details as in Fig. 65, but *L. plomleyi* sp. nov. specimen is paratype QVM 23:15465 and *T. grandis* specimen is paratype QVM 23:15557. Scale bar = 1.0 mm.

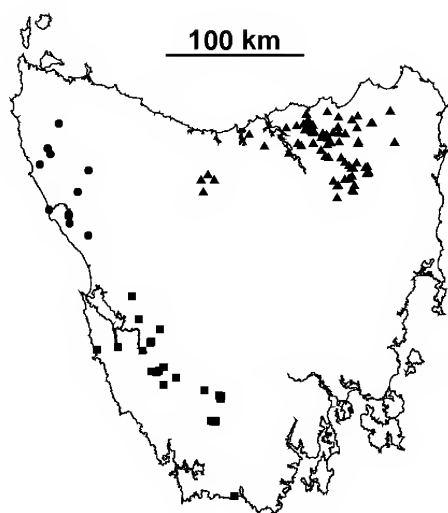


Figure 74. Localities in Tasmania of *Lissodesmus anas* sp. nov. (dots), *L. cornutus* sp. nov. (squares) and *L. devexus* sp. nov. (triangles).

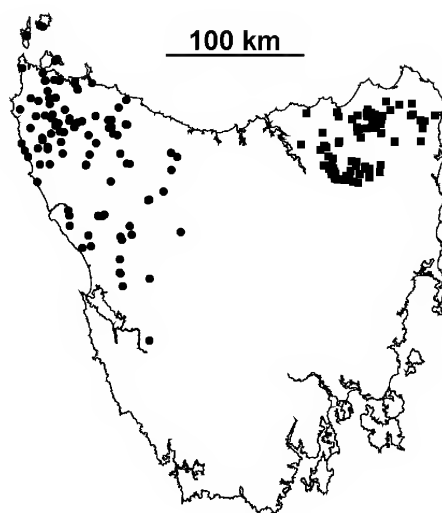


Figure 75. Localities in Tasmania of *Tasmanopeltis grandis* sp. nov. (squares) and *L. latus* sp. nov. (dots).

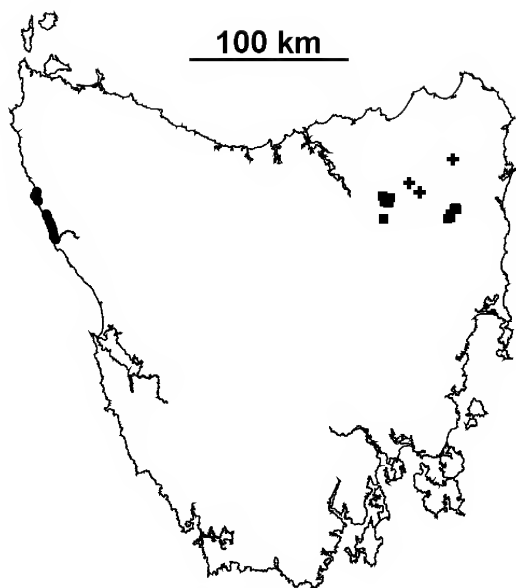


Figure 76. Localities in Tasmania of *Lissodesmus cognatus* sp. nov. (squares), *L. orarius* sp. nov. (dots) and *L. plomleyi* sp. nov. (crosses).

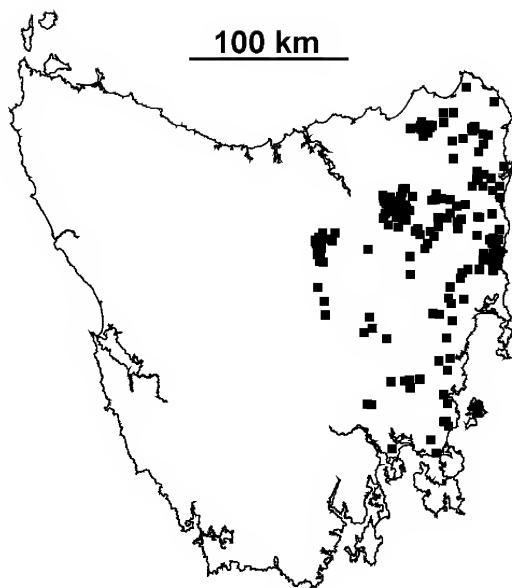


Figure 77. Localities in Tasmania of *Lissodesmus hamatus* sp. nov. (squares).

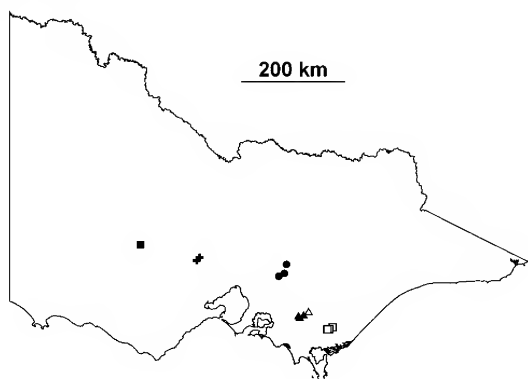


Figure 78. Localities in Victoria of *Lissodesmus blackwoodensis* sp. nov. (crosses), *L. catrionae* sp. nov. (filled square), *L. dignomontis* sp. nov. (filled triangles), *L. johnsi* sp. nov. (open triangle), *L. milledgei* sp. nov. (dots) and *L. tarrabulga* sp. nov. (open squares). For the sake of clarity, some neighbouring localities are marked with single symbols.

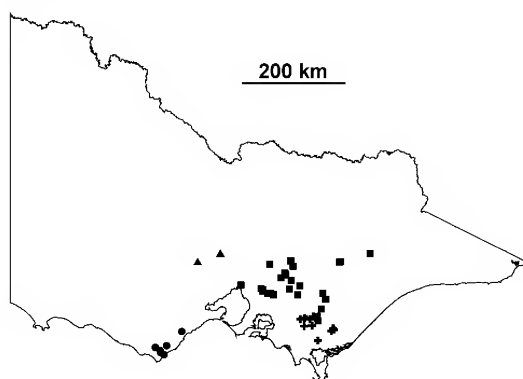


Figure 79. Localities in Victoria of *Lissodesmus gippslandicus* sp. nov. (crosses), *L. macedonensis* sp. nov. (triangles), *L. martini* sp. nov. (squares) and *L. otwayensis* sp. nov. (dots). For the sake of clarity, some neighbouring localities are marked with single symbols.



## A review of pygal-furrowed Synallactidae (Echinodermata: Holothuroidea), with new species from the Antarctic, Atlantic and Pacific oceans

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### Abstract

O'Loughlin, P.M., and Ahearn, C. 2005. A review of pygal-furrowed Synallactidae (Echinodermata: Holothuroidea), with new species from the Antarctic, Atlantic and Pacific oceans. *Memoirs of Museum Victoria* 62(2): 147–179.

We review the genera and species of pygal-furrowed Synallactidae and describe new species from the collections of the United States National Museum of Natural History (Smithsonian Institution). *Meseres* Ludwig is reviewed and placed incertae sedis. *Molpadiodemas* Heding and *Pseudostichopus* Théel are rediagnosed. *Platystichopus* Heding is declared a junior synonym of *Molpadiodemas*. *Filithuria* Koehler and Vaney and *Peristichopus* Djakonov are declared junior synonyms of *Pseudostichopus*. Lectotypes are designated for: *Meseres involutus* Sluiter, *M. macdonaldi* Ludwig, *M. peripatus* Sluiter, *Pseudostichopus globigerinae* Hérourard, *P. mollis* Théel, *P. pustulosus* Sluiter, *P. trachus* Sluiter, *P. villosus* Théel. A neotype is designated for *Pseudostichopus nudus* Ohshima.

Except for the type species, *Meseres macdonaldi* Ludwig, and *Meseres* (?) *torvus* (Théel), all species previously referred to *Meseres* are reassigned to *Molpadiodemas* or *Pseudostichopus*. *Meseres* (?) *torvus* (Théel) is retained in its original combination. Eleven new synallactid species are described: *Molpadiodemas constrictus*, *M. crinitus*, *M. epibiotus*, *M. helios*, *M. morbillus*, *M. neovillosus*, *M. pediculus*, *M. porphyreus*, *M. translucens*, *M. ustulatus* and *Pseudostichopus tuberosus*. *Molpadiodemas constrictus* is fissiparous. *Pseudostichopus villosus* var. *violaceus* Théel is raised to species status; *Pseudostichopus alatus* Imaoka, *P. trachus* Sluiter and *P. nudus* Ohshima are junior synonyms of *Pseudostichopus mollis* Théel; *Pseudostichopus globigerinae* Hérourard and *P. dilatorbis* Imaoka are junior synonyms of *Meseres* (= *Molpadiodemas*) *involutus* Sluiter; *Pseudostichopus propinquus* Fisher and *P. lapidus* Hérourard are junior synonyms of *Meseres* (= *Pseudostichopus*) *peripatus* Sluiter; and *Pseudostichopus arenosus* Ohshima and *P. molpadioides* Ohshima are junior synonyms of *Meseres* (= *Pseudostichopus*) *hyalegerus* Sluiter.

New combinations are: *Molpadiodemas atlanticus* (Perrier), *M. depressus* (Hérourard), *M. involutus* (Sluiter), *M. pustulosus* (Sluiter), *M. villosus* (Théel), *Pseudostichopus elegans* (Koehler and Vaney), *P. hyalegerus* (Sluiter), *P. papillatus* (Djakonov), *P. peripatus* (Sluiter) and *P. spiculiferus* (O'Loughlin). Other species discussed are: *Molpadiodemas violaceus* (Théel), *Pseudostichopus aemulatus* Solís-Marín and Billett, *P. echinatus* Thandar, *P. mollis* Théel, *P. occultatus* Marenzeller, and *P. profundus* Djakonov. A key is provided for the species of *Molpadiodemas* and *Pseudostichopus*. Tables are provided of genera and subgenera with current systematic status, and species with original and current combinations.

### Introduction

We report on the United States National Museum of Natural History (Smithsonian Institution) collections of synallactid holothurian species from the Atlantic, Pacific and Antarctic oceans. Only pygal-furrowed genera are dealt with. The pygal-furrowed synallactids substantially lack body wall ossicles and have a distinct pygal (posterior) vertical furrow.

Pygal-furrowed synallactids in the USNM collections comprise 345 catalogued lots (several thousand specimens) from a variety of sources. Operation Deep Freeze (USS *Edisto*) and the United States Antarctic Program (under the auspices of the

National Science Foundation, Office of Polar Programs) contributed about 47 % of the lots (research vessels USNS *Eltanin*, now the ARA *Islas Orcadas*; RV *Hero*; USCGS *Eastwind*). Between the years 1884 and 1911, the United States Fish Commission mounted expeditions to the North-west Pacific, Philippines, Hawaii, eastern Pacific, California coast, lower California and western Atlantic, and provided material (USFCS *Albatross*). When the USFC became the United States Bureau of Fisheries, cruises were conducted throughout the western Atlantic that contributed several lots from a 1970 cruise to the Gulf of Mexico (RV *Oregon II*). The Fish Commission, and later the Bureau of Fisheries, contributed about 21 % of the lots.

About 12% of the lots were provided by the Ocean Minerals Company from a benthic sampling and photographic survey of the Clarion-Clipperton Fracture Zone in the eastern central Pacific during 1978-1980 (RV *Governor Ray*).

The remaining 20% of lots were donated by various institutions, universities and agencies. A significant contribution of two new species described herein (*Molpadiodemas epibiotus* and *M. constrictus*) was made by the University of Miami from cruises in 1973 and 1975 to the Puerto Rico and Cayman Trenches (RV *Gilliss*). The Southampton Oceanographic Centre (now National Oceanographic Centre) surveys of the Western European Basin in 1979 (RV *Challenger*) and Porcupine Abyssal Plain in 1999 (RV *Discovery*) added two lots which included paratypes of the recently described *Pseudostichopus aemulatus*. Thirty lots were contributed by Oregon State University from survey cruises off the coast of Oregon in the 1960s and 1970s (RV *Commando*, RV *Cobb*, RV *Yaquina*, RV *Cayuse*). The Smithsonian Oceanographic Center, supporting the International Indian Ocean Expedition and the Southeast Pacific Benthic Oceanographic Program, added 8 lots from cruises during the 1960s to Thailand and many south-eastern Pacific localities (RV *Anton Bruun*, RV *Te Vega*). Six lots were contributed by the Woods Hole Oceanographic Institute following cruises off Argentina in 1960 (RV *Atlantis II*), to the West European Basin in 1972 (RV *Chain*), and to the North American Basin in 1973 (RV *Knorr*). Several lots were added by the Virginia Institute of Marine Science cruises to the Bahamas in 1978, 1980, and 1981 (RV *Columbus Iselin*). Texas A&M University provided one lot from a 1972 cruise to the Gulf of Mexico (RV *Alaminos*). Three lots were provided by the US Bureau of Land Management surveys off South Carolina in 1985 (RV *Cape Hatteras*), and off Louisiana during the Northern Gulf of Mexico Continental Shelf project. Fourteen lots were donated by M.D. Richardson from a survey of the Venezuelan Basin in 1981 (RV *Bartlett*). One lot was donated by the Vienna Royal Imperial Natural History Museum from a survey of the eastern Mediterranean from 1890-1894 (HMS. *Pola*). Two lots were recently donated by Dr Tohru Imaoka (ex-Seto Marine Laboratory and Faculty of Science at the Kyoto University in Shirahama), one lot by Dr Ken Smith (Scripps Institution of Oceanography) and another two lots by Dr David Stein (Systematics Laboratory, National Oceanographic and Atmospheric Administration). Two lots have insufficient information as to the source of the material.

During April 2002, Mark O'Loughlin visited the Natural History Museum in London and the Zoologisch Museum at the University of Amsterdam, and designated most of the lectotypes selected in this work. The scanning electron microscopy and most of the digital imaging were done by Cynthia Ahearn. We collaborated on systematic observations and decisions.

Because the ossicles in each pygal-furrowed synallactid species do not have a consistent form and frequently vary considerably, the SEM images selected for each species do not represent the full range of forms. They should be viewed in conjunction with the text description of forms and sizes.

In the diagnosis of *Meseres* by O'Loughlin (2002), reference was made to thin tubular appendages which are rhizomatous and sometimes branched. It is judged here that

these are epibioties, and not holothurian appendages and not species specific.

Abbreviations for institutions are: AM, Australian Museum, Sydney; BMNH, The Natural History Museum, London; MNHN, Muséum National d'Histoire Naturelle, Paris; MOM, Musée océanographique de Monaco; NMV, Museum Victoria, Australia; OMNH, Osaka Museum of Natural History, Japan; RAS, Russian Academy of Sciences, St. Petersburg, Russia; SAM, South Africa Museum, Cape Town; SMBL, Seto Marine Biological Laboratory, Kyoto University, Japan; TM, Tasmanian Museum, Hobart; UNAM, Universidad Nacional Autónoma de México; USNM, US National Museum of Natural History, Smithsonian Institution, Washington; ZMA, Zoologisch Museum, Amsterdam; ZMUC, Zoological Museum, University of Copenhagen, Denmark.

Historically, three types of registration number have been used for USNM material, and occur in this report. Prior to 1920, museum catalogue numbers without a prefix were used. In 1920, A.H. Clark began a dedicated echinoderm numbering system with the prefix E before the registration number. Since 2001, the EMU on-line system is used, and registrations reported without an E prefix.

Throughout this paper Rowe (in Rowe and Gates, 1995) is referred to as Rowe (1995). Descriptions and measurements refer to preserved material.

### History of USFCS Albatross 1906 material

Numerous holothurian types and other material collected in the north-west Pacific during the summer of 1906 by the USFCS *Albatross* cannot be located. Correspondence in the National Museum of Natural History's Registrar Office indicates that the final dispository of the material was to be the Smithsonian Institution. After the death of Dr Kakichi Mitsukuri (1909) the United States Bureau of Fisheries transferred the holothurians to his graduate student Mr Hiroshi Ohshima. He judged 46 of the 95 species and one subspecies to be new, and requested USNM catalog numbers for the type specimens for inclusion in his manuscript. The results of this study were published (Ohshima, 1915), but the specimens were not returned at the time (possibly due to World War I). In 1938, the Director of the Zoological Institute of the Tokyo Imperial University, Naohide Yatsu, discovered this collection stored in a cellar. Yatsu corresponded with Alexander Wetmore, then Assistant Secretary of the Smithsonian Institution, informing him of the holothurian collection and seeking advice as to the best way to ship the material. In April 1938 the holothurian collection in four wooden crates was transported on the *Kwansai Maru* via the Panama Canal to New York. In correspondence dated 10 June, 1938, Alexander Wetmore acknowledged receipt of the four crates in good condition.

The four crates should have been delivered to Dr Arthur H. Clark, curator of the Echinoderm Division in the NMNH. Some material was in fact returned and is now in the echinoderm collection. The fate of the remaining material is unknown. Archives have been searched for official memoranda, curators of other departments contacted, and the Natural History Museum basement and attic searched without success. Dr

Frederick M. Bayer, curator and research scientist of the Coelenterata collection, knew Dr Clark and recalled that he had many unpacked boxes in his office and that some were probably discarded.

### Key to species of pygal-furrowed Synallactidae

(The generic assignment of *Pseudostichopus profundus* Djakonov is unresolved. The species is distinguished by the unique presence of curved mesh-like narrow plates in the tube feet.)

1. Tube feet not in prominent series on paired radii; longitudinal muscles flat, broadly attached to internal body wall; gonad tubules arising from common source at end of gonoduct, branched ..... *Molpadiodemas* Heding ... 2
  - Tube feet or papillae in prominent series on paired radii; longitudinal muscles cylindrical, narrowly attached to internal body wall; gonad tubules in series along gonoduct, unbranched ..... *Pseudostichopus* Théel ... 17
2. Tube feet hair-like or thin, thread-like ..... 3
  - Tube feet cylindrical, prominent or inconspicuous .... 4
3. Body lacking brim; tube feet hair-like, over whole body, sometimes matted ventrally, anteriorly, pygally, frequently withdrawn ventrally; tentacle ossicles never plate-like rods with close fine spines ..... *Molpadiodemas villosus*
  - Body with rounded lateral brim, sometimes with pustulose bulges; tube feet soft, flaccid, thread-like, sometimes matted on small specimens, readily lost with outer body layer; tentacle ossicles include wide plate-like rods with close fine spines ..... *Molpadiodemas porphyrus*
4. Body with one, sometimes two, deep transverse constrictions; no tentacle ossicles ..... *Molpadiodemas constrictus*
  - Body lacking deep transverse constrictions; tentacle ossicles present ..... 5
5. Body typically with one or two concave depressions created by epibiotic attachments; body strongly posteriorly tapered; tentacle ossicles include thin, lumpy rods ..... *Molpadiodemas epibiotus*
  - Body lacking concavities; body not strongly posteriorly tapered; tentacle ossicles not including thin lumpy rods ... 6
6. Ventrolateral margin with distinct raised protuberances ... 7
  - Ventrolateral margin lacking distinct raised protuberances ..... 8
7. Margin serrated by transverse creasing of body; ventrolateral protuberances lacking tufts of tube feet; body wall wrinkled, with small digitate projections on low reticulate ridges; tentacle ossicles include rods; body typically encrusted with globigerines or small stones ..... *Molpadiodemas involutus*
  - Ventrolateral margin with pustules surmounted by nipple-like protuberances; tube feet in tufts on posterior pustules; body wall not wrinkled, lacking low reticulate ridges; tentacle ossicles lace mesh only; some globigerine attachments ..... *Molpadiodemas pustulosus*
8. Body wall thin, translucent; gonad ossicles predominantly thin lace mesh, not developed along primary rods ..... *Molpadiodemas translucens*
  - Body wall not translucent; gonad ossicles, if present, not predominantly thin lace mesh, if mesh, developed along primary rods ..... 9
9. Body wall thick, gelatinous; ventrolateral brim thick, rounded ..... *Molpadiodemas depressus*
  - Body wall not thick, gelatinous; lacking thick, rounded brim ..... 10
10. Cylindrical tube feet concentrated in conspicuous ventrolateral band; frequently contiguous, matted ventrolaterally ..... 11
  - Tube feet not contiguous or matted ventrolaterally ... 13
11. Tube feet typically 2.0 mm long, 0.4 mm diameter; frequently tubercles and divided pygal lobes posteriorly ..... *Molpadiodemas crinitus*
  - Tube feet typically less than 2.0 mm long, 0.4 mm diameter; lacking posterior tubercles and divisions of pygal lobes ..... 12
12. Body short, diameter large (about 2:1); tube feet typically 1.6 mm long, 0.3 mm diameter; longitudinal muscles wide; gonad ossicles long, thin rods ..... *Molpadiodemas neovillosus*
  - Body elongate, diameter small (about 5:1), long tapers distally; tube feet typically 1.0 mm long, 0.25 mm diameter; longitudinal muscles narrow; lacking gonad ossicles ..... *Molpadiodemas pediculus*
13. Tube feet cylindrical, most evident as lateral band, not matted ..... 14
  - Tube feet around body, not more evident as lateral band ... 15
14. Tube feet dark reddish brown creating a lateral spotted appearance; lacking gonad ossicles ..... *Molpadiodemas morbillus*
  - Whole body dark brown, scorched appearance; gonad ossicles present ..... *Molpadiodemas ustulatus*
15. Tube feet soft, scattered, lying all over body in larger specimens, sometimes erect orally and pygally; tentacles with large, conical, pointed peripheral digits ..... *Molpadiodemas helios*
  - Tube feet not soft, scattered, lying all over body in larger specimens; tentacle digits not large, conical, pointed ... 16
16. Even cover of small tube feet, frequently in pits or not evident, cylindrical and firm if extended; tentacle ossicles lacking knob-like central swelling; high frequency of gonad ossicles comprising rods with extensive lateral mesh ..... *Molpadiodemas atlanticus*
  - Even cover of small, soft, cylindrical tube feet, evident only on small specimens, never erect; many tentacle ossicles with knob-like central swelling; rare presence of gonad ossicles ..... *Molpadiodemas violaceus*
17. Body densely encrusted with sponge spicules or globigerines or shells or small stones ..... 18
  - Body not encrusted with attachments ..... 22
18. Body covered predominantly with dense mat of sponge spicules ..... 19
  - Body covered predominantly with globigerines (foraminiferans) or shells or stones ..... 20
19. Large dense mesh ossicles in pygal lobes; lacking gonad ossicles ..... *Pseudostichopus hyalegerus*

- Lacking mesh ossicles in pygal lobes; gonad ossicles include complex branching rods ..... *Pseudostichopus spiculiferus*
- 20. Predominantly pointed shells with globigerines and sand cover; closely knobbed tentacle rod ossicles; lacking ossicles in gonads ..... *Pseudostichopus echinatus*
- Predominantly globigerine or small stone cover; tentacle ossicles not closely knobbed rods; ossicles frequently in gonads ..... 21
- 21. Ossicles in pygal lobes and respiratory trees; pygal lobe ossicles irregular perforated plates, sometimes double layered ..... *Pseudostichopus occultatus*
- Lacking ossicles in pygal lobes and respiratory trees .... *Pseudostichopus peripatus*
- 22. Body with radial series of tubercles ventrolaterally or on paired radii ..... 23
- Body lacking radial series of tubercles ..... 24
- 23. Double series of tubercles on paired radii; ossicles present in papillae, lacking in gonads ..... *Pseudostichopus papillatus*
- Single series of lateroventral tubercles; ossicles in gonads, lacking in tube feet ..... *Pseudostichopus tuberosus*
- 24. Paired radii with long tapering papillae (frequently more than 10 mm long) ..... *Pseudostichopus elegans*
- Paired radii with short tapering papillae (up to 5.0 mm long) ..... 25
- 25. Ossicles in tube feet, perianally, lacking in gonads ..... *Pseudostichopus mollis*
- Ossicles in gonads, lacking perianally and in tube feet ... *Pseudostichopus aemulatus*

Order **Aspidochirotida** Grube, 1840

**Synallactidae** Ludwig, 1894

Table 2, Figure 1

*Remarks.* Although the Synallactidae (sensu lato) are characterized as deep-water forms that possess peltate tentacles, lack tentacle ampullae, have gonads in one or two tufts, and usually possess body wall ossicles (including tables and rods), this work embraces only those species of Synallactidae that substantially lack body wall ossicles, and have in addition a distinct pygal (posterior) vertical furrow. The pygal-furrowed Synallactidae are characterised by: a generally cylindrical body form; rounded anterior and posterior ends; ventral mouth and anus; presence of a pygal furrow; 18–20 peltate tentacles;

absence of tentacle ampullae; a complete cover of small and frequently inconspicuous tube feet; absence of retractor muscles; longitudinal muscles never divided; a solid calcareous ring; radial plates broader than high, anteriorly with a central notch and two central and two lateral low projections, posteriorly with a shallow smooth indentation and two pairs of "teeth" variably evident; interradial plates broad and low, anteriorly with a central spire, posteriorly with a smooth shallow indentation; madreporite sometimes evident externally on the anterior dorsal body surface; single, sac-like, elongate or short, ventral polian vesicle; gonad tubules in two groups, one on each side of the dorsal mesentery; respiratory trees comprising two long unequal branches of alveolar-like clusters along a central strap; ossicles absent from the body wall, but present in the pygal lobes in some species.

Body wall, pygal lobes, tube feet, tentacles, gonads, and respiratory trees were examined for ossicles in all species, and are reported only as found, not as absent. The colour of tentacles and internal anatomical features was noted throughout the study, and found to be not diagnostically reliable. The form of the peltate tentacles, which varies greatly with state of preservation, was found to be not diagnostically reliable. The presence or absence of "teeth" on the posterior indentation of the radial plates of the calcareous ring has been used diagnostically by some authors. This feature was found to be variable and subjective, and depended on the angle from which the plates were viewed. Descriptions of these features have been omitted.

The genera included in this paper have been shifted between the Gephyrothuriidae (now restricted after O'Loughlin, 1998) and Synallactidae (see O'Loughlin, 1998, 2002). In the *Zoological Catalogue of Australia* Rowe (1995) referred species of pygal-furrowed Synallactidae to the genera *Meseres* Ludwig, 1894 (incertae sedis below) and *Pseudostichopus* Théel, 1886 in the Gephyrothuriidae. Following the rediagnosis below of *Pseudostichopus* Théel, *Meseres peripatus* Sluiter, 1901 is reassigned to *Pseudostichopus*. Following examination of the AM collections by one of us (M.O'L), as far as the Australian fauna is concerned, Rowe (1995) correctly identified *Pseudostichopus mollis* Théel and *Pseudostichopus peripatus* (Sluiter) material, but wrongly identified some material as *Pseudostichopus pustulosus* Sluiter, 1901 (= *Molpadiodemas pustulosus* below). We judge that this material is *Pseudostichopus mollis*, and that *Molpadiodemas pustulosus* (Sluiter) is not to date represented in the Australian fauna.

Table 1. Index of genera and subgenera in paper, with current status including senior synonym.

Genera and subgenera	Current status or senior synonym	Family
<i>Filithuria</i> Koehler and Vaney, 1905	<i>Pseudostichopus</i> Théel, 1886	Synallactidae
<i>Meseres</i> Ludwig, 1894	<i>Meseres</i> Ludwig, 1894	Incertae sedis
<i>Molpadiodemas</i> Heding, 1935	<i>Molpadiodemas</i> Heding, 1935	Synallactidae
<i>Peristichopus</i> Djakonov, 1952	<i>Pseudostichopus</i> Théel, 1886	Synallactidae
<i>Platystichopus</i> Heding, 1940	<i>Molpadiodemas</i> Heding, 1935	Synallactidae
<i>Plicastichopus</i> Heding, 1940	<i>Pseudostichopus</i> Théel, 1886	Synallactidae
<i>Pseudostichopus</i> Théel, 1886	<i>Pseudostichopus</i> Théel, 1886	Synallactidae
<i>Trachostichopus</i> Heding, 1940	<i>Pseudostichopus</i> Théel, 1886	Synallactidae

Table 2. Index of species in paper in original combination, and with current combination or senior synonym.

Species in original combination	Current combination or senior synonym
<i>aemulatus</i> , <i>Pseudostichopus</i> , Sólís-Marín and Billett, 2004	<i>Pseudostichopus aemulatus</i> , Sólís-Marín and Billett, 2004
<i>acaudum</i> , <i>Molpadiodemas</i> , Heding, 1935	<i>Molpadiodemas atlanticus</i> (Perrier, 1898)
<i>alatus</i> , <i>Pseudostichopus</i> , Imaoka, 1990	<i>Pseudostichopus mollis</i> Théel, 1886
<i>aleutianus</i> , <i>Pseudostichopus</i> , Ohshima, 1915	<i>Pseudostichopus peripatus</i> (Sluiter, 1901)
<i>arenosus</i> , <i>Pseudostichopus</i> , Ohshima, 1915	<i>Pseudostichopus hyalegerus</i> (Sluiter, 1901)
<i>atlanticus</i> , <i>Pseudostichopus</i> , Perrier, 1898	<i>Molpadiodemas atlanticus</i> (Perrier, 1898)
<i>constrictus</i> , <i>Molpadiodemas</i> , sp. nov.	<i>Molpadiodemas constrictus</i> sp. nov.
<i>crinitus</i> , <i>Molpadiodemas</i> , sp. nov.	<i>Molpadiodemas crinitus</i> sp. nov.
<i>depressus</i> , <i>Pseudostichopus</i> , Hérouard, 1902	<i>Molpadiodemas depressus</i> (Hérouard, 1902)
<i>dilatatorbis</i> , <i>Pseudostichopus</i> ( <i>Pseudostichopus</i> ), Imaoka, 1978	<i>Molpadiodemas involutus</i> (Sluiter, 1901)
<i>echinatus</i> , <i>Pseudostichopus</i> , Thandar, 1992	<i>Pseudostichopus echinatus</i> Thandar, 1992
<i>elegans</i> , Filithuria, Koehler and Vaney, 1905	<i>Pseudostichopus elegans</i> (Koehler and Vaney, 1905)
<i>epibiotus</i> , <i>Molpadiodemas</i> , sp. nov.	<i>Molpadiodemas epibiotus</i> sp. nov.
<i>globigerinae</i> , <i>Pseudostichopus</i> , Hérouard, 1923	<i>Molpadiodemas involutus</i> (Sluiter, 1901)
<i>helios</i> , <i>Molpadiodemas</i> , sp. nov.	<i>Molpadiodemas helios</i> sp. nov.
<i>hyalegerus</i> , <i>Meseres</i> , Sluiter, 1901	<i>Pseudostichopus hyalegerus</i> (Sluiter, 1901)
<i>ingolfi</i> , <i>Plicastichopus</i> , Heding, 1942	<i>Pseudostichopus peripatus</i> (Sluiter, 1901)
<i>involutus</i> , <i>Meseres</i> , Sluiter, 1901	<i>Molpadiodemas involutus</i> (Sluiter, 1901)
<i>japonensis</i> , <i>Pseudostichopus</i> , Imaoka, 1978	<i>Pseudostichopus hyalegerus</i> (Sluiter, 1901)
<i>japonensis</i> , <i>Pseudostichopus</i> ( <i>Trachostichopus</i> ), Imaoka, 1978	<i>Pseudostichopus hyalegerus</i> (Sluiter, 1901)
<i>lapidus</i> , <i>Pseudostichopus</i> , Hérouard, 1923	<i>Pseudostichopus peripatus</i> (Sluiter, 1901)
<i>macdonaldi</i> , <i>Meseres</i> , Ludwig, 1894	<i>Meseres macdonaldi</i> Ludwig, 1894
<i>marenzelleri</i> , <i>Pseudostichopus</i> , Hérouard, 1923	<i>Pseudostichopus peripatus</i> (Sluiter, 1901)
<i>mollis</i> , <i>Pseudostichopus</i> , Théel, 1886	<i>Pseudostichopus mollis</i> Théel, 1886
<i>molpadioides</i> , <i>Pseudostichopus</i> , Ohshima, 1915	<i>Pseudostichopus hyalegerus</i> (Sluiter, 1901)
<i>morbillus</i> , <i>Molpadiodemas</i> , sp. nov.	<i>Molpadiodemas morbillus</i> sp. nov.
<i>neovillosus</i> , <i>Molpadiodemas</i> , sp. nov.	<i>Molpadiodemas neovillosus</i> sp. nov.
<i>nudus</i> , <i>Pseudostichopus</i> , Ohshima, 1915	<i>Pseudostichopus mollis</i> Théel, 1886
<i>occultatus</i> , <i>Pseudostichopus</i> , Marenzeller, 1893	<i>Pseudostichopus occultatus</i> Marenzeller, 1893
<i>occultatus</i> var. <i>plicatus</i> , <i>Pseudostichopus</i> , Koehler and Vaney, 1905	<i>Pseudostichopus peripatus</i> (Sluiter, 1901)
<i>papillatus</i> , <i>Peristichopus</i> , Djakonov, 1952	<i>Pseudostichopus papillatus</i> (Djakonov, 1952)
<i>pediculus</i> , <i>Molpadiodemas</i> , sp. nov.	<i>Molpadiodemas pediculus</i> sp. nov.
<i>peripatus</i> , <i>Meseres</i> , Sluiter, 1901	<i>Pseudostichopus peripatus</i> (Sluiter, 1901)
<i>porphyryus</i> , <i>Molpadiodemas</i> , sp. nov.	<i>Molpadiodemas porphyryus</i> sp. nov.
<i>profundi</i> , <i>Pseudostichopus</i> , Djakonov, 1952	<i>Pseudostichopus profundus</i> Djakonov, 1952
<i>propinquus</i> , <i>Pseudostichopus</i> , Fisher, 1907	<i>Pseudostichopus peripatus</i> (Sluiter, 1901)
<i>pustulosus</i> , <i>Pseudostichopus</i> , Sluiter, 1901	<i>Molpadiodemas pustulosus</i> (Sluiter, 1901)
<i>spiculiferus</i> , <i>Meseres</i> , O'Loughlin, 2002	<i>Pseudostichopus spiculiferus</i> (O'Loughlin, 2002)
<i>tachimaruae</i> , <i>Pseudostichopus</i> ( <i>Trachostichopus</i> ), Imaoka, 1978	<i>Pseudostichopus hyalegerus</i> (Sluiter, 1901)
<i>torvus</i> , <i>Stichopus</i> ?, Théel, 1886	<i>Stichopus</i> ? <i>torvus</i> Théel, 1886
<i>trachus</i> , <i>Pseudostichopus</i> , Sluiter, 1901	<i>Pseudostichopus mollis</i> Théel, 1886
<i>translucens</i> , <i>Molpadiodemas</i> , sp. nov.	<i>Molpadiodemas translucens</i> sp. nov.
<i>tuberculatus</i> , <i>Pseudostichopus</i> ( <i>Trachostichopus</i> ), Imaoka, 1990	<i>Pseudostichopus peripatus</i> (Sluiter, 1901)
<i>tuberosus</i> , <i>Pseudostichopus</i> , sp. nov.	<i>Pseudostichopus tuberosus</i> sp. nov.
<i>unguiculatus</i> , <i>Pseudostichopus</i> , Ohshima, 1915	<i>Pseudostichopus peripatus</i> (Sluiter, 1901)
<i>ustulatus</i> , <i>Molpadiodemas</i> , sp. nov.	<i>Molpadiodemas ustulatus</i> sp. nov.
<i>villosus</i> , <i>Pseudostichopus</i> , Théel, 1886	<i>Molpadiodemas villosus</i> (Théel, 1886)
<i>violaceus</i> var. <i>villosus</i> , <i>Pseudostichopus</i> , Théel, 1886	<i>Molpadiodemas violaceus</i> (Théel, 1886)

***Molpadiodemas* Heding, 1935**

## Table 1, Figure 2

*Molpadiodemas* Heding, 1935: 77–78.—Heding, 1940: 356–357.—Deichmann, 1940: 209–211.—O'Loughlin, 1998: 497.—O'Loughlin, 2002: 303, 305, 315.

*Platystichopus* Heding, 1940: 358 (new synonym).

Type species. *Molpadiodemas acaudum* Heding, 1935 (junior synonym of *Pseudostichopus atlanticus* Perrier, 1898, by O'Loughlin, 2002).

Other included species. *Molpadiodemas atlanticus* (Perrier, 1898); *M. constrictus* sp. nov.; *M. crinitus* sp. nov.; *M. depressus* (Hérouard, 1902); *M. epibiotus* sp. nov.; *M. helios* sp. nov.; *M. involutus* (Sluiter, 1901); *M. morbillus* sp. nov.; *M. neovillosus* sp. nov.; *M. pediculus* sp. nov.; *M. porphyryus* sp. nov.; *M. pustulosus* (Sluiter, 1901); *M. translucens* sp. nov.; *M. ustulatus* sp. nov.; *M. villosus* (Théel, 1886); *M. violaceus* (Théel, 1886).

**Diagnosis.** Pygal-furrowed Synallactidae displaying: absence of prominent appendages (tube feet, papillae) along the paired

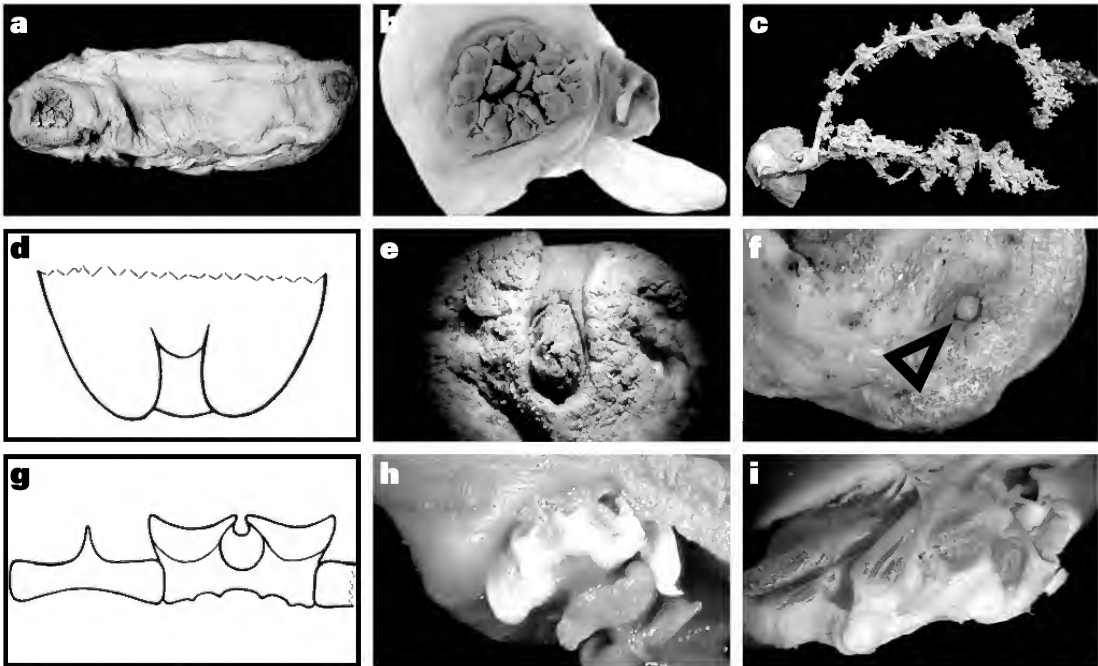


Figure 1. Characters of pygal-furrowed Synallactidae. a, ventral mouth and anus (*M. helios* sp. nov., USNM E31104, paratype, 91 mm long); b, ventral peltate tentacles, polian vesicle (*P. mollis*, TM H2004; anterior end dissected off); c, respiratory tree (*P. mollis*, TM H2004); d, drawing of dorsal posterior pygal furrow; e, posteroventral view of pygal furrow and anus (*M. violaceus*, BMNH 86.10.2.150); f, anterior dorsal madreporite (arrow) (*P. peripatus*, USNM 1008159); g, drawing of calcareous ring (radial plate right, as in *P. spiculiferus*); h, calcareous ring (*M. crinitus* sp. nov., USNM E48644, paratype); i, calcareous ring (*M. violaceus*, BMNH 86.10.2.145).

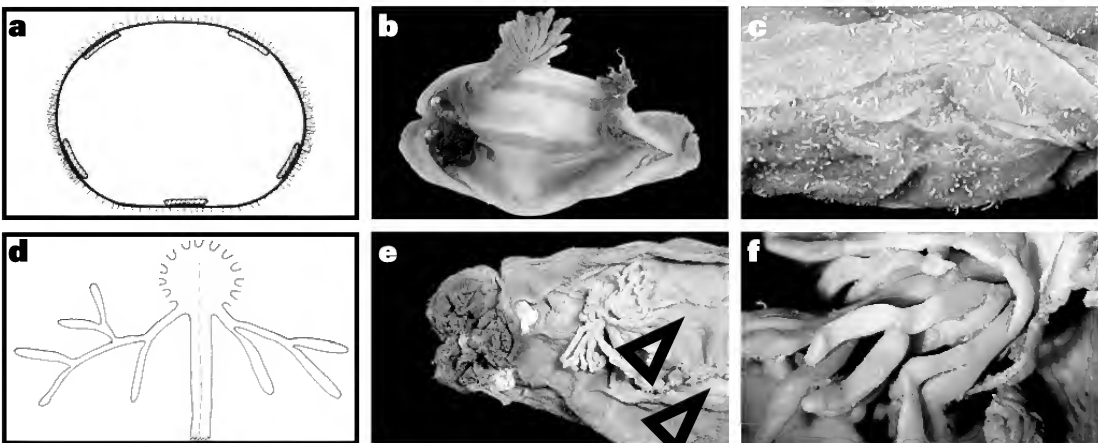


Figure 2. Characters of *Molpadiodemas*. a, drawing of transverse section of mid-body, hair-like tube foot cover, flat broadly attached longitudinal muscles (as for *M. villosus*); b, flat longitudinal muscles, gonad (upper left), respiratory tree (upper right) (*M. porphyryus* sp. nov., NMV F101871, paratype, 90 mm long); c, complete cover of tube feet (*M. translucens* sp. nov., USNM 1008072, paratype); d, drawing of part of gonad, branched tubules from common origin; e, gonad, flat longitudinal muscles (arrows) (*M. villosus*, BMNH 86.10.2.155, paralectotype); f, branched gonad tubules (*M. violaceus*, BMNH 86.10.2.145).

radii; longitudinal muscles flat, not cylindrical, broadly attached to the inner body wall; gonad tubules branched, arising from a common base on the gonoduct, not in series along the gonoduct; ossicles never present in tube feet; tentacle ossicles frequently rods with ends intertwining and side branches fused to create mesh.

**Distribution.** Cosmopolitan; 103–7086 m.

**Remarks.** Heding (1935) erected the monotypic genus *Molpadiodemas* for his new species *acaudum*, and subsequently (Heding, 1940) reassigned *Pseudostichopus atlanticus* Perrier, *P. occultatus* Marenzeller and *P. villosus* Théel to *Molpadiodemas*. O'Loughlin (1998) reassigned these four species to *Meseres* Ludwig, 1894, *Molpadiodemas* becoming a junior synonym of *Meseres*. *Molpadiodemas* is raised here out of synonymy with *Meseres* (see below under *Meseres*). O'Loughlin (2002) considered *M. acaudum* to be a junior synonym of *P. atlanticus*, and that decision is confirmed here. Heding (1940) erected the new genus *Platystichopus* for *Pseudostichopus depressus* Hérouard, 1902, which is reassigned below to *Molpadiodemas*. *Platystichopus* becomes a junior synonym of *Molpadiodemas*.

***Molpadiodemas atlanticus*** (Perrier, 1898) comb. nov.

Figures 3a, b, 4a–d, 6a, b

*Pseudostichopus atlanticus* Perrier, 1898: 1665.—Perrier, 1902: 333–338, pl. 17 figs 15–20.—Mortensen, 1927: 386–387.—Deichmann, 1930: 87–88.—Deichmann, 1940: 209, 211.—Heding, 1942: 5.—O'Loughlin, 2002: 315.

*Molpadiodemas acaudum* Heding, 1935: 78–80, pl. 6 figs 1–2.—Heding, 1940: 354–357.—Deichmann, 1940: 209, 211.—Heding, 1942: 4–5.

*Molpadiodemas atlanticus*.—Heding, 1940: 353–359.

*Meseres atlanticus*.—O'Loughlin, 1998: 497.—Thandar, 1999: 376–379, fig. 4.

*Meseres acaudum*.—O'Loughlin, 1998: 497, fig. 1g–h.

**Material examined.** *Pseudostichopus atlanticus* Perrier, 1898. Holotype. North Atlantic, off the Azores, 42°19'N, 23°31'W, 4060 m, *Talisman* stn 134, 1883, MNHN EcHh 2772. Paratype. 42°19'N, 23°36'W, 4060–4010 m, MNHN EcHh 658.

*Molpadiodemas acaudum* Heding, 1935. Paratype. North Atlantic, 60°17'N, 54°5'W, 3230 m, *Ingolf* stn 37, 1885, ZMUC.

**Other material.** Pacific Ocean, New Zealand, Chatham Is, 2610–2668 m, USNM E49319 (1); Chile, 34°07'S (incorrectly recorded as N in Théel, 1886), 73°56'W (incorrectly as E), 4069 m, *Challenger* stn 298, BMNH 1886.10.2.149 (1); 33°31'S, 74°43'W, 3950 m, *Challenger* stn 299, BMNH 1886.10.2.185 (1); Peru, 3500 m, USNM 1020067 (1); California, off Point Conception, 4100 m, 1073654 (1); Oregon, 3021 m, USNM E16475 (1); 3700 m, E16488 (3); Clipperton Fracture Zone, 13°08'–13°53'N, 129°51'–129°55'W, 4801–4923 m, E31100–E31102 (3); E31107, E31108 (2); E31121–E31123 (3); E31125 (1); E53278 (1); NMV F101845 (1).

Atlantic Ocean, Bahamas, 4828–4873 m, USNM 1021592 (10); NE of Bahamas, 4930–4940 m, E49466 (9); West European Basin, 4780–4795 m, E38320 (1); Caribbean Sea, Venezuelan Basin, 13°30'–14°50'N, 64°45'–67°30'W, 3411–5062 m, E38789–E38791 (20); E38798 (1); E39266 (20); 1023352 (1); NMV F101846 (2).

**Description.** Large, up to 210 mm long; body rounded in section, sometimes sac-like, sometimes with slight brim,

usually no detrital attachments; body wall moderately thick, soft leathery or firm gelatinous, frequently smooth surface, frequently wrinkled ventrally; uniform cover of very small tube feet, frequently not evident or in pits, most evident ventrally and pygally, from 0.1 mm long, 0.2 mm diameter up to 1.0 mm long, 0.3 mm diameter, cylindrical and firm if extended; ossicles frequently abundant in tentacles and gonads, sometimes rare or absent; tentacle ossicles frequently irregular thin rods slightly to strongly curved with ends intertwined to create small perforations, less frequently irregular straight to curved, narrow to wide, smooth to laterally spinous, variably perforated rods, ossicles variable in length, up to 500 µm long; gonad ossicles irregular rods, frequently with thin lateral branches joined to create extensive irregular lace-like mesh, non-spinous, up to 420 µm long.

**Colour.** Body and tube feet brown to grey-brown to off-white; frequently some residual mauve markings.

**Distribution.** North Atlantic, 3230–4060 m (Perrier, 1902, as *P. atlanticus*; Heding, 1935, as *M. acaudum*); south-east Atlantic, 3155–3255 m (Thandar, 1999); West European Basin, 4780–4795 m (this paper); Venezuelan Basin, 3411–5062 m (this paper); Pacific Ocean, off Chile, 3950–4069 m (Théel, 1886; see below); Pacific Ocean, 2610–4923 m (this paper).

**Remarks.** In agreement with the opinions of Deichmann (1940) and Heding (1942), *M. acaudum* was made a junior synonym of *P. atlanticus* by O'Loughlin (2002). That decision is confirmed here.

Théel (1886) noted that two *Challenger* specimens, taken in the Pacific Ocean off Chile at stations 298 and 299, closely resembled *Pseudostichopus villosus* but lacked tube feet. Both specimens were examined in this study, and determined as *P. atlanticus*. Théel (1886) reported sizes up to 280 mm long. The larger specimen is now only 150 mm long.

The very small dark brown attachments on the body which were noted by O'Loughlin (2002) and Théel (1886) are judged to be epibiotics. O'Loughlin (2002) judged the “mulberry” bodies in the body wall of *P. atlanticus*, illustrated by Perrier (1902) and Thandar (1999), and referred to by Théel (1886) as present in some specimens of *P. villosus*, to be detrital accretions and not holothurian ossicles. That opinion is maintained here.

The presence of *P. atlanticus* in the Pacific Ocean is confirmed by the numerous USNM specimens determined in this study. O'Loughlin (2002) summarised *P. atlanticus* distribution records as Atlantic Ocean only. This work extends the distribution to the Pacific Ocean, and to greater depths (at least 5062 m).

Amongst *Molpadiodemas* species the distinguishing characters of *M. atlanticus* are: large, sac-like form; even cover of small tube feet, frequently inconspicuous; frequent presence of large, irregular, open mesh-like gonad ossicles.

***Molpadiodemas constrictus* sp. nov.**

Figures 3c–e

**Material examined.** Holotype. North Atlantic Ocean, Puerto Rico Trench, 20°08'N, 65°27'W, 7086 m, RV *Gilliss*, 20 Jan 1973, USNM 1022814.



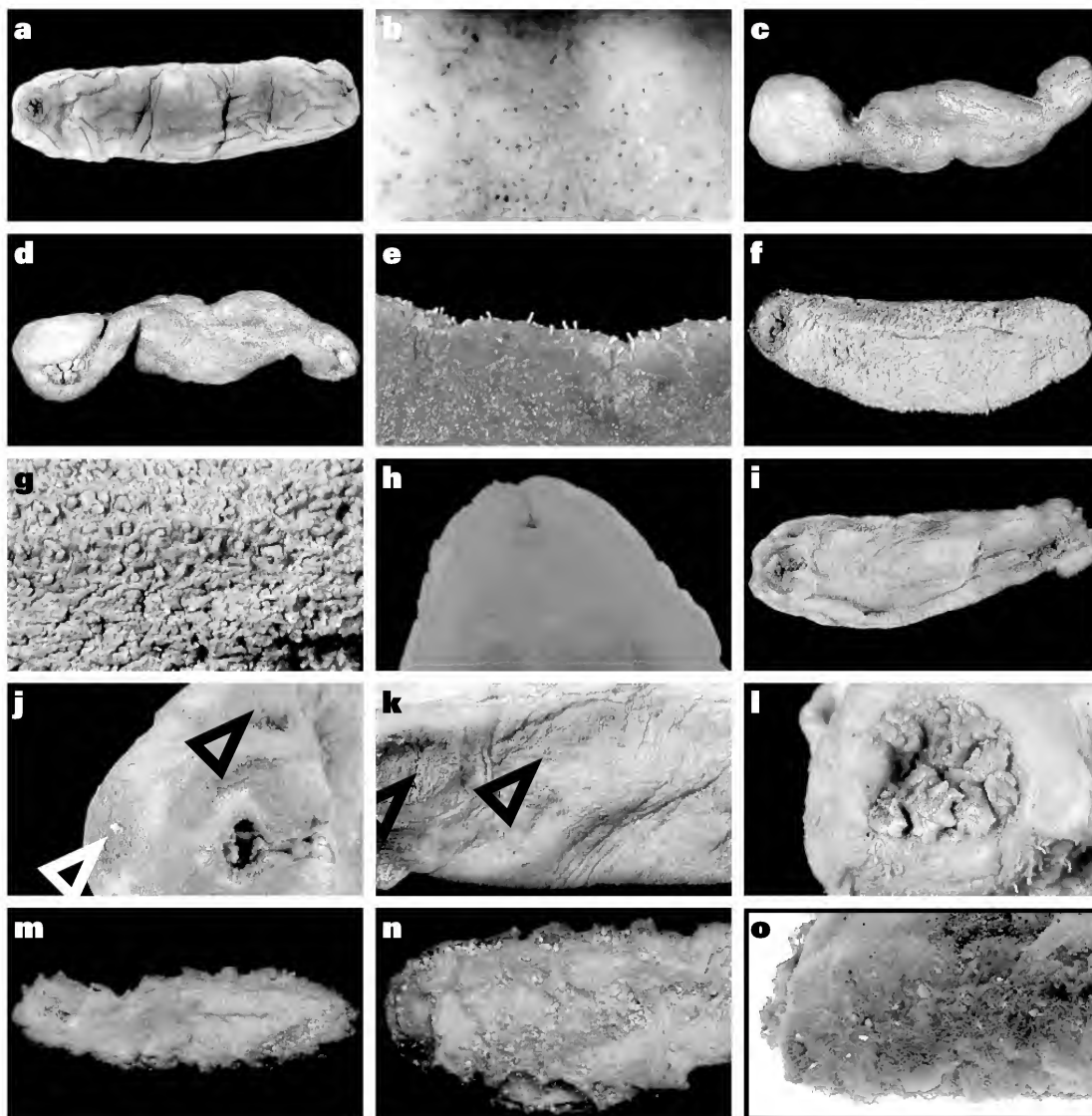


Figure 3. a–b, *M. atlanticus* (NMV F101845, 210 mm long); a, ventral view; b, small epibioties on body wall. c–e, *M. constrictus* sp. nov. (USNM 1022815, paratypes); c, dorsal view (51 mm long); d, ventral view (51 mm long); e, tube feet. f–g, *M. crinitus* sp. nov. (USNM 1023615, holotype, 96 mm long); f, ventral view; g, ventrolateral tube feet. h, *M. depressus*, pygal furrow, gelatinous body, lateral brim (NMV F101849). i–k, *M. epibiotus* sp. nov. (USNM 1008183, holotype, 110 mm long); i, ventral view, posterior taper; j, ventral mouth, epibiotie concavities (arrows); k, ventral view, epibiotie concavity (left arrow), few tube feet (central arrow). l, *M. helios* sp. nov., tentacle digits, tube feet (lower right) (USNM E31104, paratype). m–o, *M. involutus* (NMV F101850, 40 mm long); m, ventral view, serrated margin; n, dorsal anterior view, globigerines attached; o, posterior ventrolateral tube feet.

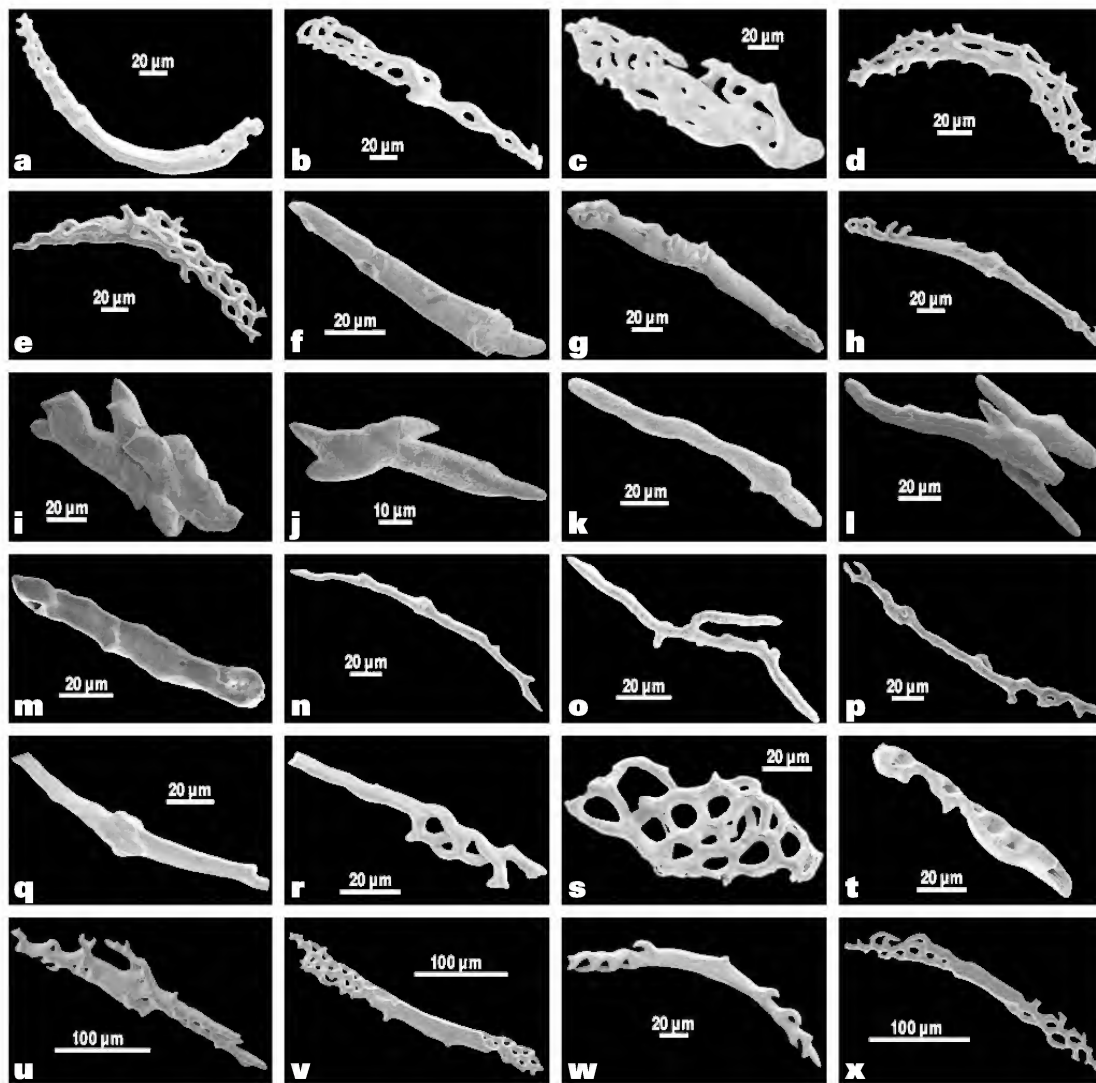


Figure 4. Tentacle ossicles (SEM). a–d, *Meseres atlanticus*, a–c (USNM E49466), d (USNM 1020067). e–h, *M. crinitus* sp. nov. (USNM E48662). i–l, *M. depressus* (USNM E53279). m–p, *M. epibiotus* sp. nov. (USNM 1008310, paratype). q–t, *M. helios* sp. nov., q–r (USNM E31104, paratype), s–t (USNM E31117, paratype). u–x, *M. involutus* (USNM E49256).

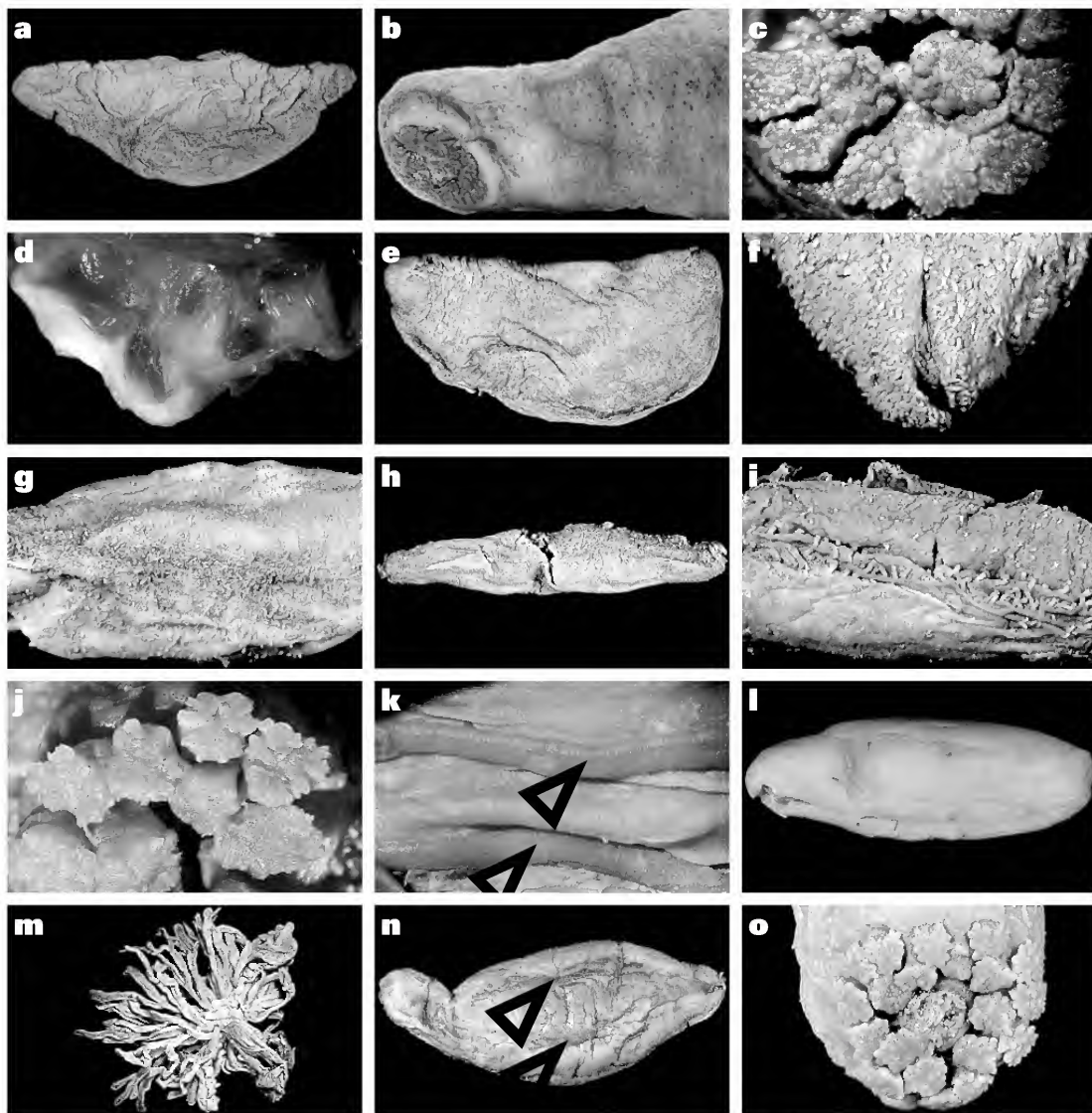


Figure 5. a–d, *Meseres morbillus* sp. nov., a, lateral view (USNM 1008093, paratype, 91 mm long); b, tentacles, ventrolateral tube feet “spotting” (NMV F101865); c, tentacles, digits (USNM E49243); d, calcareous ring (radial plate right half) (USNM 1008093, paratype). e–g, *M. neovillosus* sp. nov.; e, dorsal view (USNM 1008458, paratype, 71 mm long); f, pygal end, tube feet (USNM 1008458); g, ventrolateral tube feet (BMNH 86.10.2.151, holotype). h–k, *M. pediculus* sp. nov.; h, dorsal view, elongate form (USNM 1008318, holotype, 56 mm long); i, ventrolateral tube feet (NMV F104796, paratype); j, tentacles (holotype); k, broadly attached, relatively narrow, slightly thickened, longitudinal muscles (arrows) (paratype). l–m, *M. porphyrys* sp. nov. (USNM E38795, holotype, 114 mm long); l, dorsal view, thick rounded brim; m, gonad. n–o, *M. translucens* sp. nov. (USNM E48652, holotype, 78 mm long); n, dorsal view, longitudinal muscles visible through translucent body wall (arrows); o, tentacles.



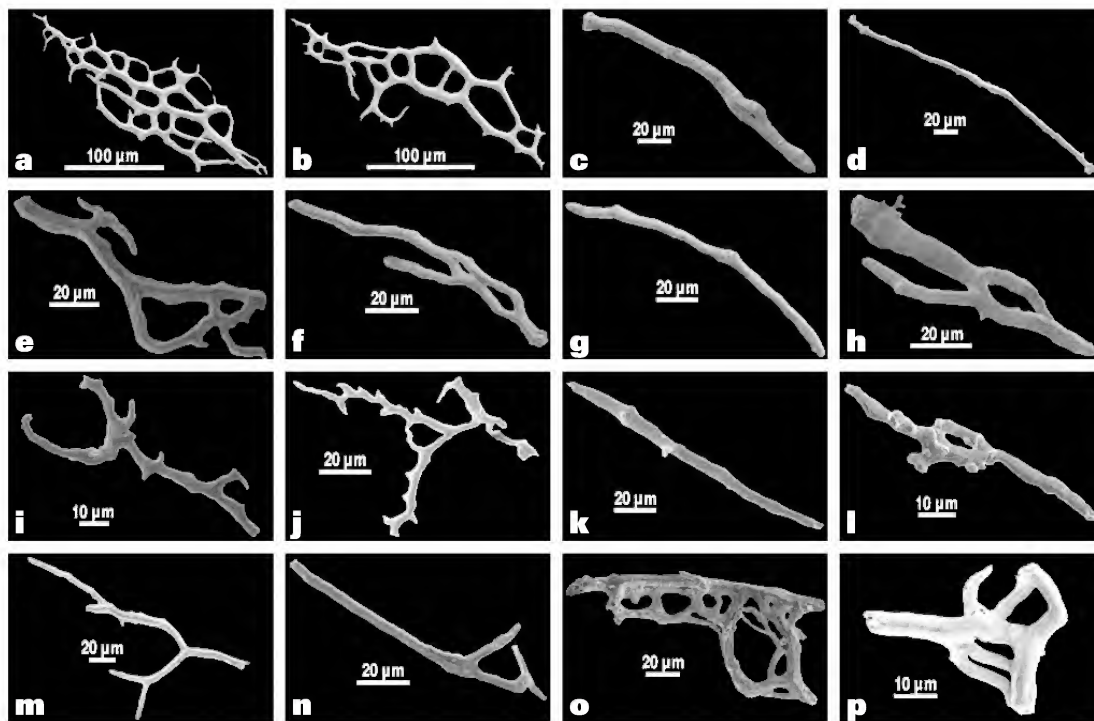


Figure 6. Gonad ossicles (SEM). a–b, *Meseres atlanticus* (USNM E53278). c–d, *M. helios* sp. nov. (USNM E31106, holotype). e–h, *M. neovillosus* sp. nov. (USNM 1008458, paratype). i–l, *M. porphyreus* sp. nov. (USNM E38795, holotype). m–p, *M. ustulatus* sp. nov. (USNM 1022493, holotype).

Paratypes. Type locality and date, USNM 1022815 (20); NMV F101857 (5).

Other material. Type locality and date, USNM 1022816 (90); NMV F101856 (10).

**Description.** Up to 62 mm long; body rounded anteriorly, frequently strongly tapered and narrow posteriorly, dorsoventrally depressed, low convex dorsally, flat ventrally frequently with longitudinal median depression, body typically with one rarely two deep transverse constrictions most frequently posterior to calcareous ring, body rounded ventrolaterally sometimes subacute; body wall thick, firm, soft, semi-gelatinous; even cover of very small tube feet all over body, some very thin erect, about 0.2 mm long, some lying on body, cylindrical, thin, typically 0.8 mm long, 0.15 mm diameter, up to 1.5 mm long, rarely contiguous; longitudinal muscles flat, broadly attached, narrow, slightly thickened; no ossicles found.

**Colour.** Body dark mauve-brown (largest), pale grey-brown to translucent (smallest), largest sometimes with dark red-brown markings dorsally, sometimes with even cover of mauve to brown spots ventrally creating a mottled appearance; largest tube feet body colour, smallest off-white.

**Etymology.** From the Latin *constrictus* (drawn together,

contracted), referring to the characteristic deep transverse constrictions on specimens.

**Distribution.** North Atlantic Ocean, Puerto Rico Trench, 7086 m.

**Remarks.** The transverse constrictions of the body are growth constrictions. They closely resemble similar growth constrictions observed by one of us (M.O'L) in the fissiparous cucumariid species *Squamocnus aureoruber* O'Loughlin and O'Hara, 1992. Emson and Wilkie (1980) listed six fissiparous holothurian species, four of them aspidochiroitids. *M. constrictus* is judged to be fissiparous.

The material was at some stage preserved in formalin solution, which might account for the complete absence of ossicles. Amongst *Molpadiodemus* species the distinguishing characters of *M. constrictus* are: body form typically with a transverse constriction; distinct posterior taper; body colour frequently with dark markings dorsally and mottled ventrally; minute thin erect tube feet; absence of ossicles.

***Molpadiodemus crinitus* sp. nov.**

Figures 1h, 3f, g, 4e–h, 7h

*Pseudostichopus* sp. MoV 2033.—O'Loughlin et al., 1994: 253–254.

*Meseres villosus*.—O'Loughlin, 2002: 313, figs 3a, b, tables 1, 2 (non *Pseudostichopus villosus* Théel, 1886).

*Material examined*. Holotype. Eastern Antarctica, Ross Sea, 72°57'S, 171°35'E, 573–576 m, USARP, *Eltanin* stn 1878, USNM 1023615.

Paratypes. Type locality and date, USNM E48644 (8); NMV F101872 (3).

Other material. Eastern Antarctica, Prydz Bay, 66°46'–68°50'S, 72°14'–77°19'E, 333–765 m, NMV F68152 (9); F68158 (1); F68162 (5); F72534 (2); F76583 (2); F76597 (1); F76606 (1); F81816–F81817 (3); Ross Sea, 67°24'–78°23'S, 166°15'E–163°02'W, 223–923 m, USNM E48578–E48580 (8); E48597 (4); E48621, E48623 (4); E48642 (6); E48646 (9); NMV F101874 (3); USNM E48662, E48663 (32); NMV F101873 (4); E49244–E49245 (12); E49270 (1); E49283 (1); E49286 (2); E49299–E49300 (3); E49368 (1); 1005125 (1); 1005129 (2); New Zealand, Antipodes Is, Campbell Plateau, 2010–2100 m, E48655 (2); W of Antipodes Is, 103 m, E49357 (4).

*Description*. Up to 150 mm long; body rounded in transverse section, lacking brim and distinctive ventrolateral margin, sometimes transverse grooves, frequently tubercles and pygal sublobes posteriorly; body wall firm, thick to thin; lacking significant globigerine or sponge spicule attachments; body covered with thick, cylindrical tube feet, typically extended, longest and often matted pygally and in a conspicuous lateral to ventrolateral band, feet typically 2.0 mm long, 0.4 mm diameter, up to 3.0 mm long, smaller and more spaced dorsally and ventrally; multiple-branching gonad tubules; ossicles in tentacles only, abundant to sparse to absent, thick irregular non-spinous rods, frequently short thick rods with bluntly rounded ends, some with swelling mid-rod, some as irregular tuberosous lumps, some with short branching, some with blunt spines, some ends branched, some branches intertwined to create perforations, lace-like mesh development on rods rare, rods up to 270 µm long.

*Colour*. Body and tube feet similar in colour, dark to pale brown, contracted tube feet rare and sometimes with dark discs.

*Etymology*. From the Latin *crinitus* (long-haired, fringed), referring to the lateral band of long, fringing tube feet.

*Distribution*. Eastern Antarctica, Prydz Bay, 333–765 m (O'Loughlin, 2002, as *Meseres villosus*); Ross Sea, 223–923 m; Antipodes Is, 103–2100 m (this paper).

*Remarks*. O'Loughlin (2002) considered Antarctic material to be *Pseudostichopus villosus*, and although it is similar in form it is not conspecific with any of the syntypes assigned to *P. villosus* by Théel (1886). Amongst *Molpadiodemas* species the distinguishing characters of *M. crinitus* are: wide ventrolateral band of thick, cylindrical, extended, sometimes matted tube feet, similar in colour to the body wall, typically 2.0 mm, long, 0.4 mm diameter; tentacle ossicles usually abundant, frequently short thick rods rounded distally; absence of gonad ossicles.

*Molpadiodemas depressus* (Hérouard, 1902) comb. nov.

Figures 3h, 4i–l

*Pseudostichopus depressus* Hérouard, 1902: 15–16, pl. 2 figs 15–18. *Platystichopus depressus*.—Heding, 1940: 353–358.

*Holotype*. North Atlantic Ocean, between Portugal and the Azores, 4360 m, Monaco stn 753, 1896, MOM (cannot be located).

*Material examined*. North Atlantic Ocean, West European Basin, 4426–4435 m, USNM 1005343 (2); NMV F101849 (1); NE of Bahamas, 4383–4558 m, USNM 1008242 (1); E53279 (21); NMV F101868 (4); Sargasso Sea, 5690 m, USNM E49454 (1); N of Puerto Rico, 5248–5278 m, USNM 1008241 (2).

Provisional (very damaged): Gulf of Mexico, 1353–1399 m, USNM E48661 (1).

*Description*. Up to 100 mm long, not tapered; body wall gelatinous, thick, firm to soft; sometimes with globigerine attachments; flat ventrally, low convex dorsally, dorsoventrally depressed; thick rounded ventrolateral brim; mouth anteroventral; dorsally smooth to wrinkled, ventrally wrinkled, pustulose; small soft tube feet all over body, thick cylindrical not thread-like, most concentrated and largest orally and pygally, up to 1.0 mm long, 0.3 mm diameter, inconspicuous and dome-like over rest of body, 0.2 mm diameter, closer ventrally than laterally and dorsally; longitudinal muscles flat, slightly thickened, narrow; ossicles in tentacles, large, thick to thin, curved to straight rods, smooth or with few blunt to sharp spines, some with mid-rod swelling, some with branched intertwined ends creating perforations, some irregularly tuberosous and rugose, some thickly bifurcate at ends, some with one or two large perforations, no lateral perforations or mesh, up to 390 µm long.

*Colour*. Body grey to off-white; tube feet off-white.

*Distribution*. North and South Atlantic Ocean, West European Basin, Sargasso Sea, off Bahamas and West Indies; 1353–5690 m.

*Remarks*. The holotype of *P. depressus* cannot be located (M. Bruni, MOM, pers. comm.), and has been missing for a long time. Belloc (1950) noted the absence when creating a catalogue of types, and there is no slide in Cherbonnier's comprehensive collection (F. Solis-Marin, pers. comm.).

Based on the description and figures of Hérouard (1902), the characteristics of *P. depressus* are: up to 74 mm long; off-white colour; pygal furrow; dorsoventrally depressed; thickened lateral brim extending around oral end; distinct dorsal madreporite plate; numerous inconspicuous tube feet all over body; narrow longitudinal muscles; two tufts of gonad tubules; lacking ossicles in body wall and gonads.

In this work numerous North Atlantic specimens are judged to be conspecific. Three were taken from the West European Basin at 4426–4435 m, a locality close to the type locality for *P. depressus* (between Portugal and the Azores, 4360 m). The conspecific material is characterized by an off-white colour, close cover of very small tube feet, absence of gonad ossicles, dorsoventral depression, and frequently a thick brim. No dorsal madreporite similar to that observed and illustrated by Hérouard (1902) for *P. depressus* has been seen. But the external evidence of a dorsal madreporite has been rare in this work, and not observing it is considered to be not significant diagnostically. Hérouard (1902) illustrated tufts but not series of gonad tubules (it is not possible to judge branching or not), and illustrated cylindrical longitudinal muscles. On the basis of the consistency of the diagnostic characters of *Molpadiodemas*

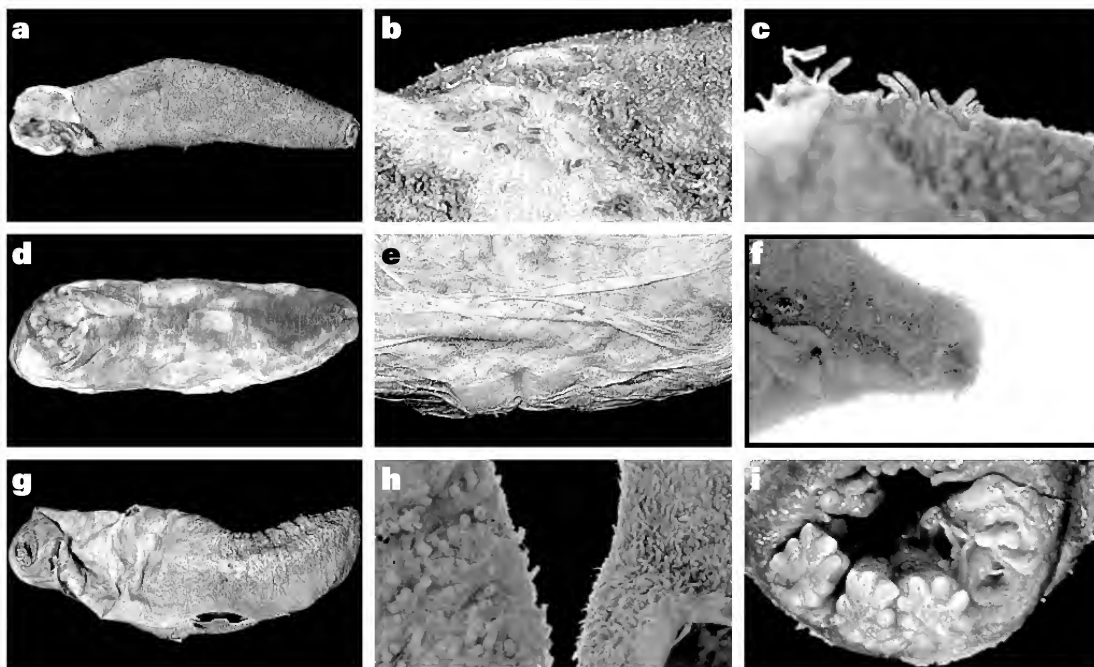


Figure 7. a–c, *Meseres ustulatus* sp. nov.; a, ventral view (USNM 1022566, paratype, 55 mm long); b, ventrolateral tube feet (USNM 1022493, holotype); c, tube feet (NMV F101858, paratype). d–f, *M. villosus*; d, ventral view (BMNH 86.10.2.147, lectotype, 90 mm long); e, ventrolateral tube feet (lectotype); f, posterior tube feet (NMV F98745). g–i, *M. violaceus* (BMNH 86.10.2.156, holotype, 142 mm long); g, ventrolateral view; h, tube feet of *M. crinitus* (left, NMV F101872, paratype) contrasted with *M. violaceus* (right, NMV F101848); i, tentacles (USNM 1022608).

(above), it is anticipated that the longitudinal muscles were broadly attached to the body wall, and that the gonad tubules were branched.

Heding (1940) erected the monotypic genus *Platystichopus* for the species *depressus*, and referred *Platystichopus* with *Benthothuria* Perrier to the Benthostichopodinae (subfamily of the Gephyrothuriidae). *P. depressus* has a distinct pygal furrow, has a close cover of minute tube feet, and lacks body wall ossicles. It shares more significant diagnostic characters with *Molpadiodemas* than *Benthothuria*, and is referred here to *Molpadiodemas*. *Platystichopus* is a junior synonym of *Molpadiodemas* (see above).

On specimens of *M. depressus* there are ventral minute red to violet conical attachments similar to those found on *M. atlanticus*, and considered here to be epibioties. Amongst *Molpadiodemas* species the distinguishing characters of *M. depressus* are: thick gelatinous grey to off-white body wall; dorsoventrally depressed body form; ventrolateral brim; thick cylindrical small tube feet; absence of gonad ossicles.

#### *Molpadiodemas epibiotus* sp. nov.

Figures 3i–k, 4m–p

**Material examined.** Holotype. North Atlantic Ocean, Caribbean Sea, Cuba, Cayman Trench, 19°39'N, 76°17'W, 6195–6320 m, RV *Gilliss*, stn GS-121, 21 Jul 1975, USNM 1008183.

Paratypes. Type locality and date, USNM 1008310 (4); NMV F101862 (1).

**Description.** Up to 125 mm long; body strongly tapered posteriorly, dorsoventrally depressed, low convex dorsally, flat ventrally; thin brim anteriorly around mouth, variably developed laterally, posteriorly; all specimens with anterior large concave depression suggesting epibiotie attachment, some smaller depressions mid-body; body wall firm, thin, soft, semi-gelatinous, embedded with white granules, surface wrinkled, additionally pustulose ventrally; complete cover of small tube feet, translucent and merged into body wall dorsally; latero-ventral tube feet in widely spaced band, sparse, subglobular, up to 0.5 mm long, 0.25 mm diameter, some with dark red markings; ventral tube feet closer, smaller, some with red markings, not extended, 0.2 mm diameter as domes; ossicles in tentacles only, abundant, variable, rods, thick to thin, lumpy to smooth to bluntly spinous, with or lacking swelling in mid-rod, limited branching at ends, some branches fused to create perforations, ossicles up to 300 µm long.

**Colour.** Dorsally off-white to greyish-white; ventrally reddish-brown around mouth, dark red flecking on surface and on some tube feet.

**Etymology.** From the Greek *epi* (upon) and *bios* (life), referring to the evidence for epibiotic attachments on all specimens.



**Distribution.** North Atlantic Ocean, Caribbean Sea, Cayman Trench, 6195–6320 m,

**Remarks.** Amongst *Molpadiodemas* species, the distinguishing characters of *M. epibiotus* are: distinctly posteriorly tapered body; dorsoventral depression of the body; presence of a thin brim anteriorly; presence of anterior concavities from epibioties; fine dark red markings ventrally on the body surface and tube feet.

***Molpadiodemas helios* sp. nov.**

Figures 1a, 3l, 4q–t, 6c, d

**Material examined.** Holotype. Central Pacific Ocean, Clipperton Fracture Zone, 13°13'N, 129°53'W, 4877 m, RV *Governor Ray*, Ocean Minerals Co., 15 Feb 1980, USNM E31106.

Paratypes. Type locality, 13°13'N, 129°52'–53'W, 4724–4892 m, 1980, USNM E31104 (1), E31117 (1), E31134 (1), E31137 (1), E31141 (1), NMV F101852 (1), F101854 (1).

Other material. Type locality, 13°13'N, 129°52'–55'W, 4755–4938 m, 1980, USNM E31097 (1), E31103 (1), E31105 (1), E31110–E31114 (5), E31118 (1), E31129 (2), E31133 (1), E31138–E31140 (3), E31144 (1), E48515 (1), NMV F101853 (1).

**Description.** Up to 170 mm long; body wall soft-leathery to semi-gelatinous; no body attachments (encrustations); body rounded in transverse section, lacking brim; tentacles with about 10 large conical pointed digits peripherally, some digits bifid; tube feet soft, white to semi-translucent, scattered and lying all over body, most dense around oral and pygal areas, up to 2.0 mm long, 0.15 mm diameter, frequently cylindrical digitate erect orally and pygally, typically 0.8 mm long, 0.2 mm diameter; ossicles in tentacles and gonad; tentacle ossicles sparse to rare, thick to thin rods up to 150 µm long, rare branches, rare perforations at ends or branches joined to form perforations, lacking spines, sometimes swollen mid-rod; gonad tubules with abundant irregular thin rods, some irregularly branched, branches sometimes joined to create perforations, lacking spines, swellings rare, up to 280 µm long.

**Colour.** Body off-white to grey, frequently semi-translucent, smaller specimens sometimes with pale brown.

**Etymology.** From the Greek *helios* (sun), referring to the sun-flower appearance of the radiating tentacle digits.

**Distribution.** Central Pacific Ocean, Clipperton Fracture Zone, 13°13'N, 129°53'W, 4724–4938 m.

**Remarks.** Amongst *Molpadiodemas* species, the distinguishing characters of *M. helios* are: relatively prominent soft tube feet scattered over the body, sometimes cylindrical and erect posteriorly and anteriorly; prominent conical tentacle digits; predominantly smooth rod ossicles in gonad.

***Molpadiodemas involutus* (Sluiter, 1901) comb. nov.**

Figures 3m–o, 4u–x

*Meseres involutus* Sluiter, 1901a: 11–12.—Sluiter, 1901b: 49–50, pl. 8 fig. 6.—Perrier, 1902: 359. (*Meseres convolutus*) [lapsus].—O'Loughlin, 2002: 306, fig. 2e, tables 1, 3, 4.

*Pseudostichopus globigerinae* Hérouard, 1923: 23–25, pl. 4 fig. 6.—Mortensen, 1927: 386–388.—Deichmann, 1930: 87, 90.

*Pseudostichopus (Pseudostichopus) globigerinae*.—Heding, 1940: 353–360.—Imaoka, 1978: table 1–1.—Thandar, 1992: 167.

*Pseudostichopus villosus*.—Hansen, 1956: 47–48 (part; non *Pseudostichopus villosus* Théel, 1886).

*Pseudostichopus (Pseudostichopus) dilatorbis* Imaoka, 1978: 378–380, 384, fig. 1 B–E, table 1–1 (new synonym).

*Meseres globigerinae*.—O'Loughlin, 2002: 305, tables 1, 3 (new synonym).

**Material examined.** *Meseres involutus* Sluiter. Lectotype (designated here). Indonesia, Sawu Sea, 10°49'S, 123°23'E, 918 m, *Siboga* stn 300, ZMA V.Ech.H1052. Paralectotype. Seram Sea, 3°27'S, 131°01'E, 567 m, *Siboga* stn 173, ZMA V.Ech.H1051 (1).

*Pseudostichopus globigerinae* Hérouard, 1923. Lectotype (larger syntype, with pygal furrow, designated here). North Atlantic, off Newfoundland, 46°18'N, 50°42'W, 4380 m, Monaco stn 2964, 20 Jul 1910, MOM (examination via pers. comm. by M. Bruni at MOM). Second syntype, type locality and date, MOM.

*Pseudostichopus (Pseudostichopus) dilatorbis* Imaoka, 1978. Holotype. Japan, W of Kyushu, near Shimo-Koshiki I., 400–450 m., SMBL 309.

Other material. Pacific Ocean, eastern Australia, Tasman Sea, Lord Howe Rise, 1423 m, AM J23326 (1); off Newcastle, 2984–3058 m, J16833 (1); off Nowra, 1650–1750 m, NMV F80451 (1); Japan, East China Sea, off Kagoshima, 420 m, USNM 1071585 (3), NMV F104793 (2); 300–330 m, USNM 1071802 (1); Galapagos, 3667 m, USNM E950 (1).

Atlantic Ocean, West European Basin, 4426–4435 m, USNM 1005340 (8); NMV F101850 (2); off South Carolina, 2100 m, USNM E41392 (3); NMV F101851 (1); Gulf of Mexico, 1668 m, USNM E46796 (3); off Louisiana, 2063–2085 m, USNM 1008165 (2); NMV F101869 (1); 1829 m, USNM E46798 (2); 1646 m, E46799 (1).

South Atlantic Ocean, Argentina, Buenos Aires, SE of Mar Del Plata, 5208–5223 m, USNM 1005317 (1); 1008207 (1); off Falkland Is, 5687–5801 m, E49256 (5); E49359 (1); Scotia Sea, 2250–2404 m, E49295 (2).

**Description.** Up to 155 mm long; typically encrusted with globigerine or small stone attachments; body usually dorso-ventrally depressed; flat ventrally, low convex dorsally; margin subacute, partly serrated because of transverse creasing of body wall, sometimes narrow rounded brim; body wall thin to thick, firm, wrinkled, with small digitate projections on low reticulate ridges; raised protuberances ventrolaterally, pygally; close cover of thin cylindrical tube feet, sometimes larger and more evident and reddish-brown in ventrolateral band, sometimes matted, typically 1.0 mm long, 0.2 mm diameter, up to 3.0 mm long, 0.5 mm diameter; multiple branching gonad tubules; ossicles in tentacles only, sometimes not detected; ossicles unbranched rods with thick central swelling and branched rods, branches frequently intertwining at ends or joining laterally to create irregular perforated mesh, ossicles up to 330 µm long.

**Colour.** Body grey to off-white; tube feet sometimes reddish-brown ventrolaterally.

**Distribution.** Indonesia, Seram and Sawu Seas, 567–918 m (Sluiter, 1901a); eastern Australia, Tasman Sea, 1423–3058 m (O'Loughlin, 2002); Japan, W of Kyushu, 400–450 m (Imaoka, 1978; as *P. dilatorbis*); East China Sea, off Kagoshima, 300–420 m (this paper); Galapagos Islands, 3667 m (this paper); northern Atlantic Ocean, off Newfoundland, 4380 m (Hérouard, 1923, as *P. globigerinae*); West European Basin,

4426–4435 m; western Atlantic Ocean, off South Carolina, Gulf of Mexico, 1646–2100 m; southern Atlantic Ocean, off Argentina, 5208–5223 m; Falkland Is, 5687–5801 m; Scotia Sea, 2250–2404 m (this paper).

**Remarks.** Sluiter (1901a) described two syntypes, and both were examined during a visit to the University of Amsterdam (Apr 2002). One is designated above as the lectotype.

Hansen (1956) considered *P. globigerinae* to be a junior synonym of *P. villosus*. O'Loughlin (2002) rejected the synonymy on the evidence that *P. villosus* never has tufts of tube feet on tubercles along the posterior margin, or a globigerine cover, or translucent body wall. A further synonymy was not suggested. Based on the description by Hérourard (1923), on observations communicated by Michèle Bruni (MOM), and on photographs by Francisco Solis-Marin (UNAM) of a tentacle ossicles slide prepared by Gustav Cherbonnier (MNHN box 108 slide 44), the characters of the larger syntype are: up to 30 mm long; body completely covered by globigerines; body wall thin, soft, translucent; pygal furrow present; villous-like cover of unequal and unevenly distributed small tube feet, rare mid-ventrally, in tufts on posterior ventrolateral tubercles creating serrated appearance; flat longitudinal muscles; lacking gonad; and tentacle ossicles branched closed mesh fragments. O'Loughlin (2002) noted that there was inadequate descriptive information to confirm any synonymy, but in the light of further data *P. globigerinae* is considered here to be a junior synonym of *M. involutus*.

Hérourard noted that there was no pygal furrow on the 15 mm long smaller syntype of *P. globigerinae*, and M. Bruni observed a cylindrical longitudinal muscle. The smaller of the two syntypes is not conspecific with *P. globigerinae*, but cannot be identified. The larger syntype is designated above as lectotype.

The description of *P. dilatorbis* by Imaoka (1978) refers to the external characters of the large paratypes and the internal characters of the holotype. The holotype has the diagnostic characters of *Molpadiodemas*; the paratypes those of *Pseudostichopus*. Although the holotype lacks tentacles ossicles, several specimens of *Pseudostichopus dilatorbis* recently donated by Tohru Imaoka yielded abundant tentacle ossicles and possess external characters similar to those of *M. involutus*. *Pseudostichopus dilatorbis* is considered here to be a junior synonym of *Molpadiodemas involutus*. The two paratypes of *P. dilatorbis* are much larger (up to 180 mm long) than the holotype, and are very close in appearance and diagnostic characters to the types of *Pseudostichopus trachus* Sluiter, 1901, which is considered below to be a junior synonym of *Pseudostichopus mollis*. The paratypes are referred below to *P. mollis*.

Material determined here extends the distribution of *M. involutus* from the western Pacific Ocean into the eastern Pacific Ocean, northern and southern Atlantic Ocean and Scotia Sea.

Amongst *Molpadiodemas* species, the distinguishing characters of *M. involutus* are: body wall with small digitate projections on low reticulate ridges; margin partly serrated because of transverse creasing of body wall; cylindrical tube feet most

evident in ventrolateral band; tentacle ossicles rods and mesh on primary rods; typical dense cover of globigerines.

***Molpadiodemas morbillus* sp. nov.**

Figures 5a–d, 8a–d

**Material examined.** Holotype. Antarctic Ocean, South Shetland Is, Bransfield Strait, Livingston I., 62°38'S, 59°37'W, 681–1409 m, RV *Eltanin*, USARP Cr 6 stn 430, 7 Jan 1963, USNM E48647.

Paratypes. Type locality and date, USNM 1008093 (31); NMV F101866 (5).

Other material. Scotia Sea, 55°01'–59°37'S, 26°00'–45°05'W, 1071–3040 m, USNM E48601 (4); E48653 (3); E49243 (10); NMV F101865 (3); USNM E49251 (1); E49253 (12); E49254 (49); NMV F101867 (5); USNM 1008094–1008096 (7); 1022457 (9); 1022461 (1); South Sandwich Trench, 5350 m, USNM 1071583 (8); South Shetland Is, 884–935 m, USNM 1005127 (2); 2119–2562 m, E48569 (1); W of Elephant I., 2672–3020 m, E48625 (1); N of Amundsen Sea, 4682 m, USNM 1022460 (1); 4866–4881 m, E48649 (2); 4709 m, E48650 (1); NW of Amundsen Sea, 4575–4813 m, E48631 (1).

**Description.** Up to 143 mm long; body tapered anteriorly and posteriorly, frequently rounded in transverse section, sometimes with transverse folds and ridges; ventrolateral margin commonly rounded, sometimes with distinct serrated margin created by transverse folds; body wall firm, soft, thin (small to medium specimens) to thick (largest specimens), surface wrinkled and pustulose; some specimens with grit or globigerine attachments; complete cover of scattered small tube feet, predominantly not extended, frequently evident as a broad ventrolateral band, frequently extended and close pygally, frequently lost with loss of outer body wall, cylindrical not thread-like when extended, not villous or matted, sometimes contiguous pygally, never ventrolaterally, typically 0.5 mm long, 0.2 mm diameter pygally and when extended ventrolaterally, 0.2 mm diameter when contracted; ossicles in tentacles only, abundant to sparse to absent, irregular rods, thick to thin to wide, some perforated, frequently narrow rods with large central knob and pointed ends, some long thin rods with closely intertwined branches at ends, some with short branches, some with blunt spines, up to 300 µm long.

**Colour.** Body reddish-brown to brown, smallest grey, largest off-white; tube feet typically dark reddish-brown to chocolate, creating a spotted appearance.

**Etymology.** From the Latin *morbillus* (measles), referring to the typically spotted body appearance created by the dark-coloured tube feet.

**Distribution.** Amundsen Sea, Scotia Sea, 681–4881 m.

**Remarks.** One specimen was covered by a rhizomatous epibiotte with vertical tongue-like stems, that could be mistaken as a character of the species, *M. morbillus* is similar to *M. crinitus* (above), from which it is distinguished by: smaller, usually contracted, tube feet (thick and extended in *M. crinitus*, typically 2.0 mm long, 0.3 mm diameter, up to 3.0 mm long, 0.5 mm diameter); tube feet which are scattered and never contiguous ventrolaterally (often matted ventrolaterally in *M. crinitus*); and tube feet which are darker in colour than the body wall (same colour as body wall in *M. crinitus*).

Table 3. Revised systematic status of the ten syntypes of *Pseudostichopus villosus* Théel, 1886 and variety *P. villosus* var. *violaceus* Théel, 1886.

Challenger	BMNH Registration	Type status	Revised systematic status
stn 244	86.10.2.147	Lectotype	<i>Molpadiodemas villosus</i> (Théel, 1886)
stn 157	86.10.2.155	Paralectotype	<i>Molpadiodemas villosus</i> (Théel, 1886)
stn 156	86.10.2.156	Holotype	<i>Molpadiodemas violaceus</i> (Théel, 1886)
stn 61	86.10.2.145 (2)	Syntypes	<i>Molpadiodemas violaceus</i> (Théel, 1886)
stn 147	86.10.2.154	Syntype	<i>Molpadiodemas violaceus</i> (Théel, 1886)
stn 325	86.10.2.150	Syntype	<i>Molpadiodemas violaceus</i> (Théel, 1886)
stn 216	86.10.2.151	Holotype	<i>Molpadiodemas neovillosus</i> sp. nov.
stn 302	86.10.2.153	Syntype	<i>Pseudostichopus</i> ? <i>peripatus</i> (Sluiter, 1901)
Unconfirmed (small specimens):			
stn 146	86.10.2.148	Paralectotype	<i>Molpadiodemas villosus</i> (Théel, 1886)
stn 156	86.10.2.146	Paralectotype	<i>Molpadiodemas villosus</i> (Théel, 1886)
stn 296	86.10.2.152	Paralectotype	<i>Molpadiodemas villosus</i> (Théel, 1886)

Amongst *Molpadiodemas* species, the distinguishing characters are: conspicuous ventrolateral band of small dark cylindrical tube feet which create a spotted appearance; tentacle ossicles irregularly present, frequently narrow rods, tapered at ends, with central knob; absence of gonad ossicles.

#### *Molpadiodemas neovillosus* sp. nov.

Table 3, Figures 5e–g, 6e–h, 8e, f

*Pseudostichopus villosus* Théel, 1886: 170–171 (part; syntype from Challenger stn 216 only; non *Pseudostichopus villosus* Théel, 1886, lectotype designated below).

*Material examined.* Holotype. Syntype, *P. villosus* Théel, 1886. Northern Pacific Ocean, Caroline Is, 2°56'N, 134°11'E, 3658 m, Challenger stn 216, 16 Feb 1875, BMNH 86.10.2.151.

Paratypes. Galapagos Is, 2°34'N, 92°6'W, 2487 m, USNM 18275 (1); NMV F101847 (1); 4°33'S, 87°42'W, 3667 m, USNM 1008458 (1).

Other material. North Pacific Ocean, Mexico, S of Punta Maldonado, 3436 m, USNM 18276 (1).

*Description.* Up to 70 mm long; body rounded in transverse section, narrower anteriorly and posteriorly, lacking tubercles on pygal lobes, lacking brim; body wall thin, smooth, thicker and wrinkled if contracted, lacking globigerine or sponge spicule attachments; tube feet in conspicuous ventrolateral wide band, continuous anteriorly and pygally, feet cylindrical, frequently overlapping and matted, typically 1.6 mm long, 0.3 mm diameter; tube feet smaller, more spread, dorsally, smallest ventrally; broad, flat longitudinal muscles about 4.0 mm wide; multiple branching gonad tubules; ossicles in tentacles and gonads; tentacle ossicles abundant rods, variable form, predominantly thin, curved, smooth to rugose, not spinous, blunt to tapered, frequently intertwined at ends, rarely branched or with slight mid-rod swelling, some with lateral fused branches creating narrow mesh, rods up to 320 µm long; gonad ossicles abundant rods, predominantly thin, long, rarely branched, straight to slightly bent to irregular, rarely with slight swelling mid-rod, up to 350 µm long.

*Colour.* Body and tube feet pale brown to off-white.

*Etymology.* From the Latin *neo* (new, recent), referring to this recently recognized new species with villous ventrolateral tube feet.

*Distribution.* Central Pacific Ocean, Caroline and Galapagos Is, Mexico, 2487–3667 m.

*Remarks.* Théel (1886) commented specifically on this specimen, noting that “the individual obtained at Station 216 is remarkable in that the pedicels of the dorsal surface and the sides of the body are slightly thicker and larger than those of the ventral surface which are thread-like and very minute”. Further to this comment is the observation that the tube feet are largest and most dense and frequently matted in a wide ventrolateral band which extends around the anterior and posterior ends of the body.

Amongst *Molpadiodemas* species, the distinguishing characters are: ventrolateral band of villous cylindrical tube feet that are distinctly smaller than those of the similar *M. crinitus* (above); tentacle ossicles predominantly thin curved rods with intertwined ends, some with slight swelling centrally; gonad ossicles abundant thin, short to very long, rods.

#### *Molpadiodemas pediculus* sp. nov.

Figures 5h–k, 8g–h

*Material examined.* Holotype. South Atlantic Ocean, NE of South Sandwich Is, 55°07'S, 25°59'W, 5435–5453 m, RV *Eltanin*, Cr 8 stn 591, 29 Apr 1963, USNM 1008318.

Paratypes. Type locality and date, NMV F104796 (1).

Other material. Scotia Sea, N of South Orkney I., 2800 m, USNM E48635 (1).

*Description.* Up to 60 mm long; body small, rounded in section, elongate, tapered anteriorly and posteriorly, lacking brim; body wall firm, semi-gelatinous, surface smooth, not covered with attachments; tube feet all over body, overlapping ventrolaterally, distinctly cylindrical, frequently erect, close cover, anteriorly and pygally, typically 1.0 mm long, 0.25 mm diameter, up to 1.5 mm long; tube feet typically shorter, more thread-like, dorsally and ventrally than ventrolaterally; longitudinal muscles broadly attached, relatively narrow, slightly thickened; some unbranched gonad tubules; ossicles in tentacles only, predominantly irregular, thick, rough to smooth, sometimes bluntly spinous rods, swollen mid-rod, tapering at ends, rare branches joined to create thick intertwining mesh, sometimes irregularly tuberos, up to 280 µm long.

**Colour.** Body, tube feet off-white to pale brown.

**Etymology.** From the Latin *pediculus* (little foot), referring to the prominent ventrolateral band of small tube feet.

**Distribution.** South Atlantic Ocean, off South Sandwich and South Orkney Is, 2800–5453 m.

**Remarks.** Amongst *Molpadiodemas* species, the distinguishing characters are: body tapering orally and anally; close cylindrical tube feet overlapping ventrolaterally; longitudinal muscles broadly attached, relatively narrow, slightly thickened.

***Molpadiodemas porphyus* sp. nov.**

Figures 2b, 5l, m, 6i–l, 8i–l

**Material examined.** Holotype. North-west Atlantic Ocean, Caribbean Sea, Venezuelan Basin, 13°30'N, 64°45'W, 3459–3503 m, Norda Thru IRCZM, RV *Bartlett* 1301-82, 27 Nov 1981, USNM E38795.

Paratypes. Type locality, date, depth, USNM 1008206 (1); NMV F101870 (1); type locality, 3428–3476 m, USNM E38792 (1); NMV F101871 (1); type locality, 3422–3464 m, USNM E38797 (2).

Other material. Type locality, date, 3476–3518 m, USNM E38793 (2); 3967–4009 m, USNM E38799 (1); Caribbean Sea, off Cuba, 2997 m, E2589 (1); South-west Atlantic Ocean, off Brazil, 1227 m, E2584 (14).

**Description.** Up to 115 mm long; body wall thick, firmly gelatinous; some globigerines attached, no overall cover; to varying degrees flattened dorsoventrally, distinct rounded brim laterally, sometimes with slightly pustulose bulges; body covered with small soft flaccid thread-like tube feet, usually spread, sometimes matted in smaller specimens, readily lost with loss of outer body layer, typically 0.7 mm long, 0.15 mm diameter, pygally up to 1.0 mm long, 0.2 mm diameter; ossicles in tentacles and gonad; tentacle ossicles numerous, variable, curved thin spinous rods (predominant in small specimens), closely finely spinous and smooth unbranched thick to broad plate-like rods, sometimes perforated, sometimes branched and intertwined at ends, spinous or smooth mesh, up to 270 µm long; gonad ossicles abundant to sparse, small thin rods, bluntly spinous or smooth or knobbed, branched or unbranched, some branching creating narrow mesh, up to 140 µm long.

**Colour.** Very soft outer body layer brown, thick semi-gelatinous layer grey with distinct overall violet mauve hue, some sparse violet mauve colour spots; tube feet off-white.

**Etymology.** From the Greek *porphyro* (purple), referring to the violet mauve colour hue and colour spots.

**Distribution.** North-west and South-west Atlantic Ocean, Caribbean Sea, and off Brazil; 1227–4009 m.

**Remarks.** Amongst *Molpadiodemas* species, the distinguishing characters are: firm thick gelatinous body wall; lateral brim; grey-mauve colouration; thread-like flaccid tube feet; tentacle ossicles frequently closely bluntly spinous.

***Molpadiodemas pustulosus* (Sluiter, 1901) comb. nov.**

*Pseudostichopus pustulosus* Sluiter, 1901a: 16–17.—Sluiter, 1901b: 53–55, pl. 4 fig. 1, pl. 9 fig. 1.

**Material examined.** Lectotype (designated here). Indonesia, Halmahera Sea, 0°45'S, 128°40'E, 827 m, *Siboga*, stn 145, ZMA V.Ech.H1012. Paralectotypes. Lectotype locality and date, ZMA V.Ech.H1011 (1); Ceram Sea, 3°38'S, 131°26'E, 924 m, *Siboga* stn 170, ZMA V.Ech.H1006 (1).

**Description.** Up to 115 mm long; some globigerines attached; distinct ventrolateral margin with series of nipple-like pustules, most conspicuous posteriorly and around anus on lobes of pygal furrow, some pustules lobed; body covered with elongate tube feet, present but not extended mid-ventrally; tube feet clustered in tufts on posterior pustules; gonad tubules short, fat, multiple-branching; ossicles in tentacles only; tentacle ossicles non-spinous lace mesh, comprising thin branched joined rods, not perforated plates.

**Distribution.** Indonesia, Halmahera and Ceram Seas, 827–924 m.

**Remarks.** During an examination (Apr 2002) of the holothurian types in the University of Amsterdam, four specimens were found to be registered as syntypes of *P. pustulosus*. This was in accord with the catalogue published by Jangoux (1991). But only three syntypes were recorded by Sluiter (1901a). One of the four, registered and recorded by Jangoux (1991) as ZMA 1303 from Station 170, was not conspecific with the other syntypes. Sluiter (1901) reported, and Jangoux (1991) listed, two syntypes of *P. trachus*, but the syntype registered as ZMA E2496/2 was missing from the collection. The extraneous syntype of *P. pustulosus* (ZMA 1303) was conspecific with the syntype of *P. trachus*, and is now registered as a *P. trachus* type (ZMA V.Ech.H2496/2, following the catalogue registration number of Jangoux, 1991). A lectotype of *P. pustulosus* is designated above.

The designated lectotype is the specimen figured by Sluiter (1901b), and does not show all of the characters referred to here in the description. The syntype showing the diagnostic characters most completely, such as the tube feet, is the smallest (ZMA V.Ech.H1006; 63 mm long).

Rowe (1995) judged that *Pseudostichopus propinquus* Fisher, 1907 and *Pseudostichopus nudus* Ohshima, 1915 were junior synonyms of *P. pustulosus*. *M. pustulosus* has the diagnostic characters of *Molpadiodemas* (above), not *Pseudostichopus* (below). Both synonymies are rejected on the grounds of the relevant generic diagnostic characters. *P. propinquus* and *P. nudus* are discussed below. Rowe (1995) identified material from off Newcastle on the eastern Australian slope as *Pseudostichopus pustulosus*. All Australian slope material has been examined and none determined as *P. pustulosus*. Material from off Newcastle (AM J16749) was determined as *P. mollis* (below).

Amongst *Molpadiodemas* species, the distinguishing characters of *M. pustulosus* are: conspicuous nipple-like pustules on the ventrolateral margin; tufts of tube feet on the pustules posteriorly; lace-mesh tentacle ossicles.

***Molpadiodemas translucens* sp. nov.**

Figures 2c, 5n, o, 8m–p, 12e, f

**Material examined.** Holotype. Weddell Sea, Antarctic Peninsula, 64°07'S, 40°48'W, 4465–4557 m, RV *Eltanin*, USARP Cr 12 stn 1018, 21 Mar 1964, USNM E48652.

Paratypes. Type locality and date, USNM 1008072 (5); NMV F101863 (2).

Other material. South-east Pacific Basin, 4575–4813 m, E49487 (2).

**Description.** Up to 79 mm long; body wall thin, soft, translucent; no body attachments; body typically rounded in transverse section, not elongate, tapered anteriorly and posteriorly, lateroventral margin sometimes subacute or slightly bulbous; complete body cover of small, cylindrical, soft, scattered tube feet, erect or lying on body, typically 0.3 mm long, 0.1 mm diameter, rarely contiguous over most of body, slightly more concentrated ventrolaterally, most concentrated and frequently contiguous pygally, typically 0.6 mm long, 0.2 mm diameter; longitudinal muscles flat, slightly narrow; ossicles in tentacles and gonads; tentacle ossicles abundant, variable in form, thin to thick tapered smooth distally bluntly pointed rods sometimes with central rounded thickening, rods with intertwined branched ends creating small perforations, rods with fused side branches creating small lateral perforations, fused branches sometimes creating large perforated irregular mesh, ossicles up to at least 520  $\mu$ m long; gonad ossicles abundant, predominantly thin lace mesh with irregular large perforations, not developed on primary thick rod, some irregular finely spinous thin rods with irregular branching closing to create perforations, ossicles up to 320  $\mu$ m long.

**Colour.** Pale greyish brown, with traces of mauve colouration; tube feet off-white to semi-translucent.

**Etymology.** From the Latin *lux* (light) and *trans* (through), referring to the translucent body wall.

**Distribution.** South-east Pacific Basin, Weddell Sea, Antarctic Peninsula, 4465–4813 m.

**Remarks.** Amongst *Molpadiodemas* species, the distinguishing characters are: translucent body wall; lace mesh gonad ossicles.

***Molpadiodemas ustulatus* sp. nov.**

Figures 6m–p, 7a–c, 12q–t

**Material examined.** Holotype. South-east Pacific Ocean, Peru, Peru-Chile Trench, 8°48'S, 80°40'W, 5069–5173 m, RV *Anton Bruun*, Cr 11 stn 178, 3 Nov 1965, USNM 1022493.

Paratypes. Type locality and date, USNM 1022566 (3); NMV F101858 (1).

**Description.** Up to 73 mm long; form cylindrical, narrowly elongate, slightly dorsoventrally depressed (possible artefact), lacking brim; outer body wall soft, pustulose, wrinkled; inner body wall soft, thin, semi-gelatinous; close cover of small cylindrical tube feet all over body, extended but not erect, longest and most evident in lateral band, not matted, up to 1.0 mm long, typically 0.6 mm long, 0.2 mm diameter; ossicles in tentacles and gonad; tentacle ossicles abundant smooth rods, thick to thin, straight to curved, some with central swellings, some with short branches, some with intertwined joined ends creating large and small perforations, some irregularly tuberosous, up to at least 270  $\mu$ m long; gonad ossicles numerous thick to thin smooth rods, some lateral branches fused to form mesh with large perforations, fragments up to 280  $\mu$ m long.

**Colour.** Body and tube feet very dark brown.

**Etymology.** From the Latin *ustulatus* (scorched), referring to the dark brown blistered appearance of the specimens.

**Distribution.** South-east Pacific Ocean, Peru-Chile Trench, 5069–5173 m.

**Remarks.** The specimens are in poor condition, but adequate for establishing morphological diagnostic characters. Amongst *Molpadiodemas* species the distinguishing characters of *M. ustulatus* are: very dark brown colour; narrowly elongate body; tube feet most evident in lateral band; gonad rod ossicles with open lateral mesh.

***Molpadiodemas villosus* (Th  el, 1886) comb. nov.**

Table 3, Figures 2a, e, 7d–f, 8q–t, 12a–d

*Pseudostichopus villosus* Th  el, 1886: 170–171 (part; syntypes from *Challenger* stns 157, 244 only; not *Pseudostichopus villosus* var. *violaceus* Th  el, 1886).

**Material examined.** Lectotype (designated here). North-west Pacific Ocean, off Japan, 35°22'N, 169°53'E, 5304 m, *Challenger* stn 244, BMNH 86.10.2.147.

Other material. Paralectotype, Southern Indian Ocean, 53°55'S, 108°35'E, 3566 m, *Challenger* stn 157, BMNH 86.10.2.155 (1).

Northern Pacific Ocean, Clarion-Clipperton Fracture Zone, no depth, USNM E48492 (1); Galapagos Is, 3667 m, E9929 (1); South-east Pacific Basin, N of Amundsen Sea, 5042–5045 m, USNM 48659 (3); 4709 m, E49280 (1); 4676 m, E48584 (1); 4740–4742 m, E49333 (5); N of Marie Byrd Land, 4682 m, E48658 (1); Ross Sea, 3495–3514 m, E48583 (4); 2005–2010 m, E48620 (7); NMV F101859 (2).

North Atlantic Ocean, North American Basin, 3264–3356 m, USNM 1006292 (1).

Scotia Sea, S of South Georgia I., 3413–3446 m, USNM E48634 (1); E48633 (8); NMV F98745 (2); 2742–2758 m, USNM E48640 (2); NMV F101860 (2); 2384–2416 m, USNM E49257 (1, with commensal gastropods); South Georgia I., 3166–3255 m, USNM E48609 (1); South Shetland Is, 681–1409 m, E48571 (2); N of Bellingshausen Sea, 4941 m, E48589 (1).

**Description.** Up to 110 mm long; body variably elongate and tapered anteriorly and posteriorly; subcylindrical, lacking brim, sometimes sac-like; lacking globigerine or sponge spicule or grit attachments; body wall thick semi-gelatinous to thin firm, surface smooth to wrinkled and pustulose; tube feet small, soft, hair-like, never erect, close to sparse cover over whole body, dorsally typically 1.5 to 2.0 mm long, up to 3.0 mm long, 0.05 mm diameter; tube feet sometimes matted ventrolaterally, anteriorly and pygally, typically 1.0 to 1.3 mm long, 0.2 mm diameter; ventral tube feet frequently withdrawn, if extended typically 0.5 mm long, 0.2 mm diameter; gonad tubules unbranched and multibranched; ossicles in tentacles and gonad; tentacle ossicles abundant, variable form, large, up to 530  $\mu$ m long, frequently rods perforated entire length, rods variably with mid-rod swelling, thick rods with branches at ends intertwined to create mesh, thick rods with lateral joined branches creating mesh, large mesh ossicles (intertwined, joined rods, not perforated plates), club-shaped rods with minute perforations, smooth thick to thin rods tapered at ends, sometimes blunt spines, some knots of thick irregularly branching rods; gonad ossicles abundant, long thin branched and unbranched

irregular rods, many with lateral mesh with large perforations, many thick smooth rods with central knobbed swelling, many central knobs elongating into short thick branches which fuse to create perforations, up to 270  $\mu$ m long.

**Colour.** Greyish-white, sometimes with reddish-brown hue; tube feet off-white, sometimes pale brown ventrolaterally.

**Distribution.** Atlantic, Indian, Pacific and Southern Oceans, Ross Sea, N of Amundsen Sea, N of Bellingshausen Sea, Scotia Sea; 681–5304 m.

**Remarks.** Théel (1886) listed ten syntypes of *P. villosus* (nominal subspecies *villosus*), plus a type of his variety *P. villosus* var. *violaceus*. All have been examined in this study. Théel noted the “villosus” appearance of the specimen from stn 244 and it is this one we have chosen as lectotype. One other, from stn 157, is a paralectotype. Of the others, the one from stn 216 is not conspecific and is described above as the new species, *M. neovillosus*.

Four of the remaining types are also not *P. villosus*. The type of the variety and three of the syntypes are referred below to the species *Molpadiodemas violaceus* (Théel, 1886). The seventh syntype (Southern Pacific Ocean, off Chile, 42°43'S, 82°11'W, 2652 m, *Challenger* stn 302, BMNH 86.10.2.153) is not *P. villosus*. It was 80 mm long, and had a close cover of globigerines, strong transverse ridges ventrally, an acute serrated ventrolateral margin, and cylindrical longitudinal muscles. No gonad was present. It is probably *Pseudostichopus peripatus* (Sluiter), but there is insufficient evidence to confirm a determination. The three remaining syntypes are small, and remain unconfirmed paralectotypes: stn 146, BMNH 86.10.2.148 (1); stn 156 (of two lots from this Station the lot with the *P. villosus* syntype), BMNH 86.10.2.146 (1); stn 296, BMNH 86.10.1.152 (1).

Dr Frank Rowe (pers. comm.) observed eggs or embryos amongst the tentacles of the paralectotype (stn 157), and considered the possibility of brood-protection. The observation was confirmed during this study.

The distribution of *P. villosus* given by O'Loughlin (2002) is not valid, since only one of the syntypes is conspecific with the designated lectotype, and most previous determinations of *P. villosus* are in doubt.

Amongst *Molpadiodemas* species, the distinguishing characters are: close to sparse body cover of small, hair-like, off-white tube feet, sometimes matted ventrolaterally and pygally; gonad ossicles.

### *Molpadiodemas violaceus* (Théel, 1886) comb. nov.

Table 3, Figures 1e, i, 2f, 7g–i, 8u–x

*Pseudostichopus villosus* var. *violaceus* Théel, 1886: 172, pl. 10 fig 6b (raised to species status here).

*Pseudostichopus villosus* Théel, 1886: 170–171 (part; syntypes from *Challenger* stns 61, 147, 325; non *Pseudostichopus villosus* Théel, 1886).

**Material examined.** Holotype. *Pseudostichopus villosus* var. *violaceus* Théel, 1886. Southern Ocean, off Shackleton Ice Shelf, 62°26'S, 95°44'E, 3612 m, *Challenger* stn 156, BMNH 86.10.2.156.

Other material. *Pseudostichopus villosus* Théel, 1886. Syntypes. North-western Atlantic Ocean, 34°54'N, 56°38'W, 5212 m, *Challenger* stn 61, BMNH 86.10.2.145 (2); southern Indian Ocean, off Crozet I., 46°16'S, 48°27'E, 2926 m, *Challenger* stn 147, BMNH 86.10.2.154 (1); south Atlantic Ocean, off Argentina, 36°44'S, 46°16'W, 4846 m, *Challenger* stn 325, BMNH 86.10.2.150 (1).

Weddell Sea, S of South Orkney Is, 3587–3660 m, USNM E48600 (1); 1008106 (4); NMV F101844 (2).

South Atlantic Ocean, Scotia Sea, South Orkney Is, 2196 m, USNM E49337 (2); 3250–3285 m, E48651 (11); NMV F101843 (2); Burdwood Bank, 3514–3642 m, USNM E48627 (1); 4026–4063 m, E48654 (2); South Sandwich Is, 5435–5453 m, E48637 (6); NMV F101842 (2); 4758 m, E48626 (1); 1190–1469 m, 1022456 (3); Drake Passage, 3788–3944 m, USNM 1008117 (1); 2324–3020 m, E48591 (1).

South Pacific Ocean, Chile, depth unknown, USNM E48636 (1); Peru-Chile Trench, 6006 m, E48611 (1); 6146–6354 m, 1022608 (2); NMV F101848 (1); 5069–5173 m, USNM 1022609 (1); SE Pacific Basin, 4731 m, E48630 (3); 4773 m, E49334 (1); 3859 m, E48657 (3); 4572–4848 m, E49366 (1); 3694 m, E48605 (2); 4682 m, 1022455 (1).

**Description.** Up to 220 mm long; body wall leathery, pliable, surface folded and wrinkled, sometimes mucilaginous; sparse small grit and globigerine attachments; body rounded in transverse section, tapered anteriorly, posteriorly, frequently sac-like; ventrolateral margin rounded, not distinctive, lacking brim, mouth terminal ventral; even cover of small soft cylindrical tube feet all over body, never erect, evident in small specimens only, slightly larger anteriorly and pygally, may be matted, typically 1.0 mm, long, 0.3 mm diameter, frequently withdrawn in small pits, not evident on smooth leathery body wall of largest specimens; ossicles in tentacles abundant, rare in gonad; tentacle ossicles variable, predominantly bluntly tapered rarely curved unbranched smooth thick rods with distinct knob-like central swelling, some rods lacking central swelling, some rods with bifurcate or intertwined ends, some with lateral and terminal perforations, rare blunt spines and knobs, rods frequently 250  $\mu$ m long, up to 350  $\mu$ m long; gonad ossicles rarely present, straight and irregular sometimes bluntly spinous short thin rods, some with central swelling, some branching creating perforations, never mesh ossicles, up to 150  $\mu$ m long.

**Colour.** Brown to grey-brown to off-white; tube feet brown to pale brown to off-white.

**Distribution.** Atlantic, southern Indian and Pacific, and Southern Oceans, Weddell Sea, Scotia Sea, SE Pacific Basin, 2196–6354m.

**Remarks.** Théel (1886) established ten syntypes for *Pseudostichopus villosus*, and a holotype for *P. villosus* var. *violaceus*. Three of the ten syntypes of *P. villosus* are conspecific with the type of *P. villosus* var. *violaceus*.

Amongst *Molpadiodemas* species, the distinguishing characters are: leathery body wall; tube feet inconspicuous in large specimens, when small even cover of soft cylindrical tube feet with some anterior and pygal matting; tentacle ossicles frequently thick smooth bluntly-tapered rods, many with large knob-like central swelling; rare presence in gonad of short, thin rod ossicles.

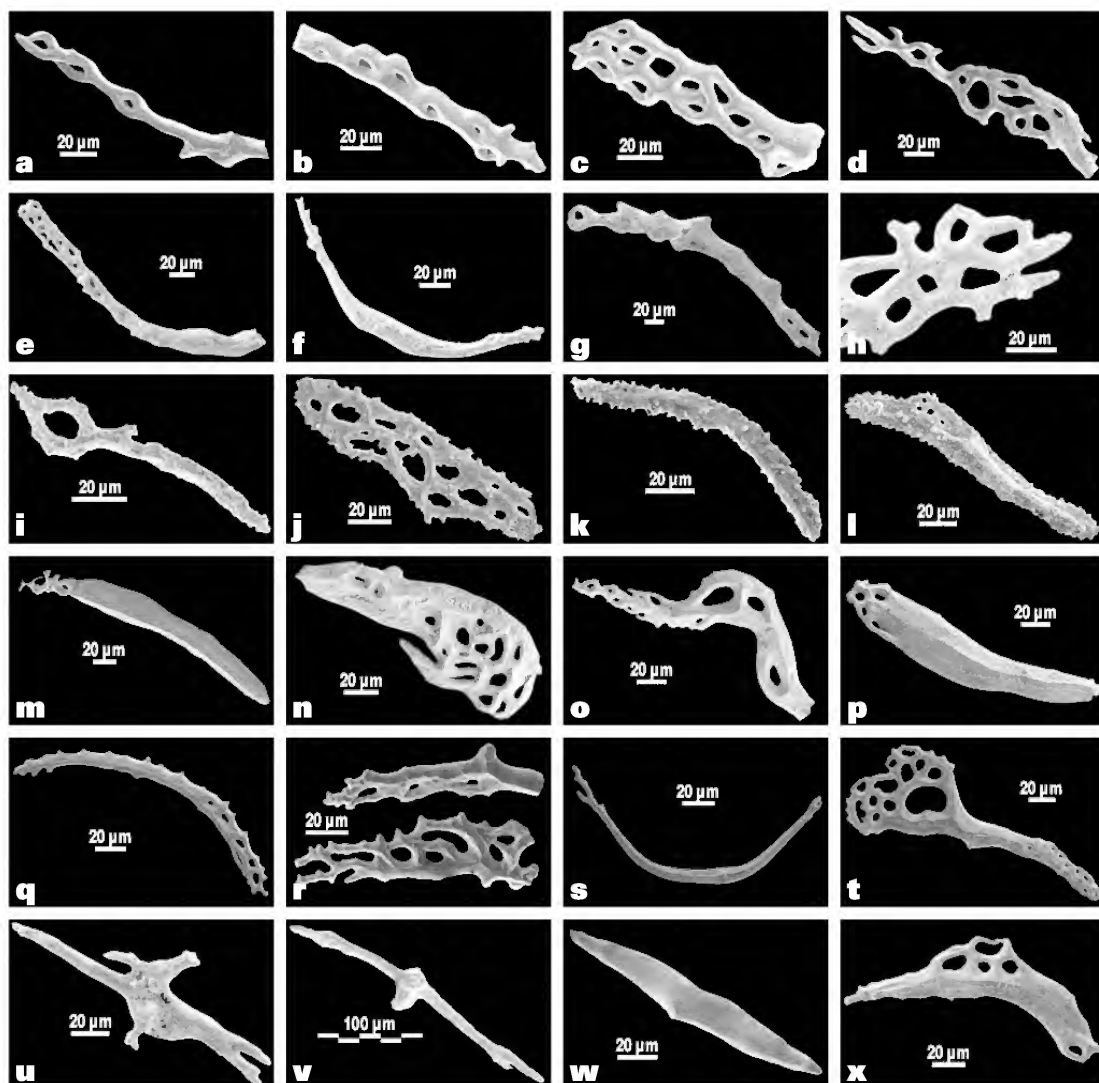


Figure 8. Tentacle ossicles (SEM). a–d, *Meseres morbillus* sp. nov. (USNM E49251). e–f, *M. neovillosus* sp. nov. (USNM 1008458, paratype). g–h, *M. pediculus* sp. nov. (USNM 1008318, holotype). i–l, *M. porphyus* sp. nov. (USNM E38795, holotype). m–p, *M. translucens* sp. nov. (USNM E48652, holotype). q–t, *M. villosus*, q–r (USNM E48640), s–t (USNM E9929). u–x, *M. violaceus*, u–v (USNM 1022608), w–x (USNM E49366).



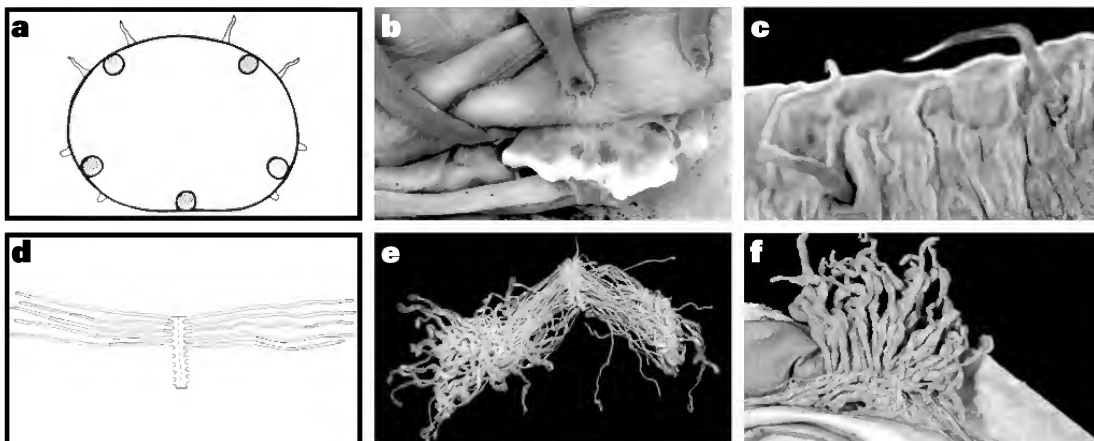


Figure 9. Characters of *Pseudostichopus*. a, drawing of transverse section of mid-body (as in *P. mollis*); b, cylindrical longitudinal muscles detached from calcareous ring (*P. tuberosus* sp. nov., NMV F101864, paratype); c, dorsolateral radial papillae (*P. elegans*, NMV F97447, papillae up to 8 mm long); d, drawing of part of gonad, unbranched tubules, arising separately along gonoduct; e, two series of unbranched gonad tubules along gonoduct (*P. mollis*, TM H2004); f, gonad (*P. tuberosus* sp. nov., paratype, USNM 1008333).

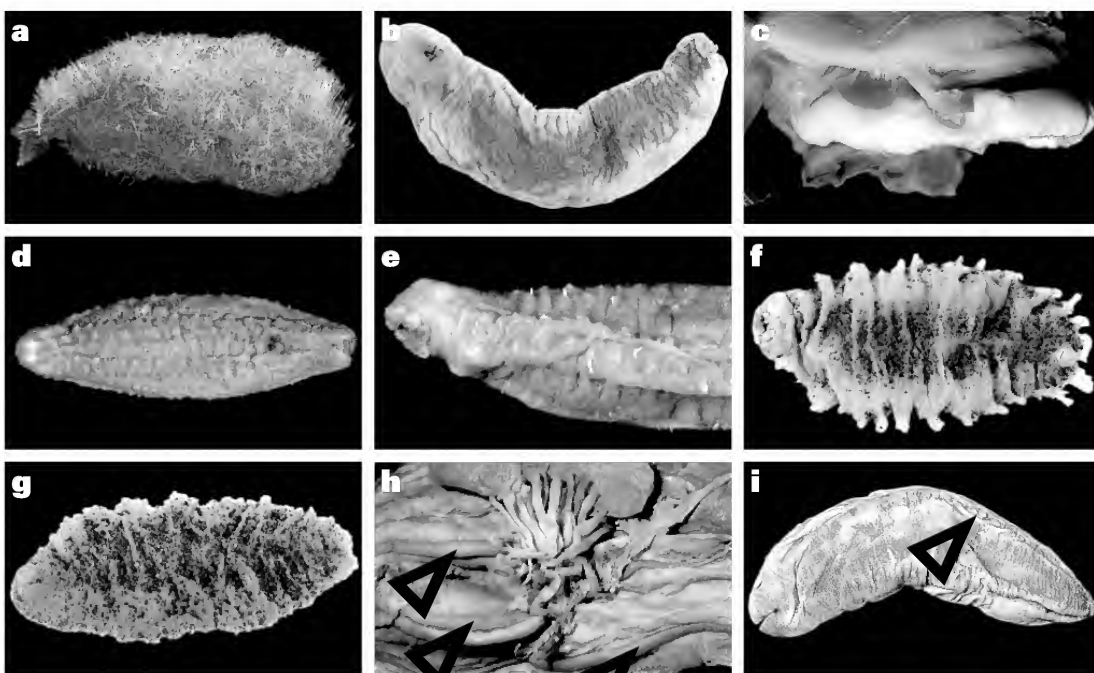


Figure 10. a, *Pseudostichopus hyalegerus*, sponge spicule cover (*P. japonensis*, paratype, SMBL 314, junior synonym, 29 mm long). b–c, *P. mollis*; b, rugose ventrum (TM H3111, 145 mm long); c, calcareous ring (TM H2004). d–e, *P. papillatus* (RAS, syntype, 27 mm long); d, dorsal view of paired radial tubercles; e, ventrolateral view, tube feet. f–h, *P. peripatus*; f, ventral view, marginal tubercles, grit attachment, transverse creases (NMV F101840, 60 mm long); g, ventral view, marginal tubercles, grit attachment, transverse creases (NMV F101839, 45 mm long); h, cylindrical muscles (arrows), gonad tubules (*P. tuberculatus*, holotype, OMNH Iv1190, junior synonym). i, *P. tuberosus* sp. nov. (USNM E16721, holotype, 115 mm long), ventral view, lateroventral tubercles (arrow).

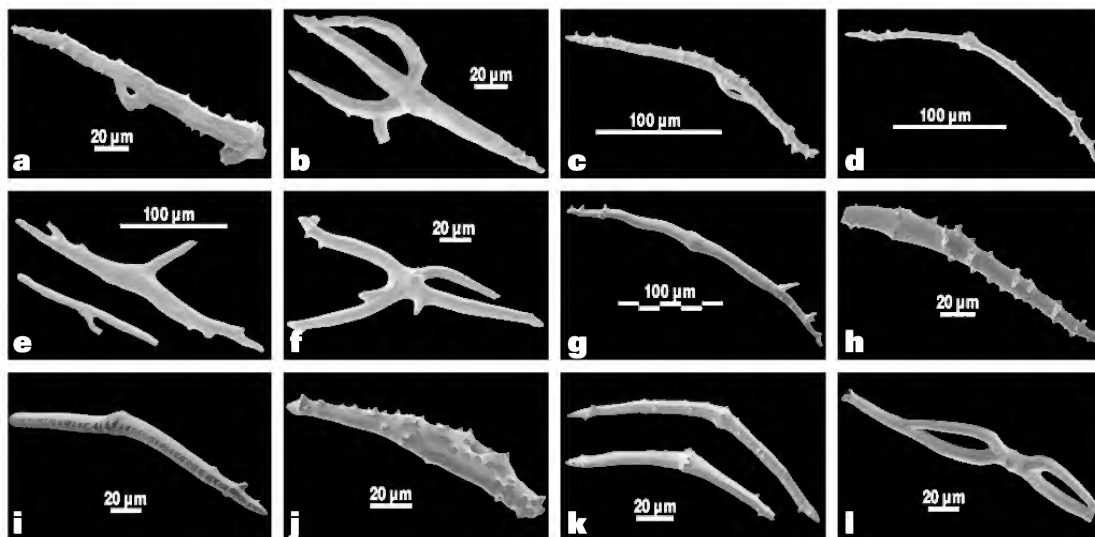


Figure 11. Tentacle ossicles (SEM). a–b, *Pseudostichopus aemulatus* (USNM 1025525, paratype). c–d, *P. elegans* (USNM E16505). e–f, *P. mollis* (USNM E48656). g–h, *P. tuberosus* sp. nov. (USNM E16721, holotype). i–l, *P. peripatus*, i (USNM 12198), j (USNM E38794), k (USNM E38796), l (USNM E49349).

### *Pseudostichopus* Théel, 1886

#### Table 1, Figure 9

*Pseudostichopus* Théel, 1886: 169.—Ludwig, 1894: 38.—Perrier, 1902: 337–338.—Hérouard, 1902: 11.—Fisher, 1907: 691.—Mitsukuri, 1912: 3.—Hérouard, 1923: 21–23.—Ekman, 1925: 32–36.—Ekman, 1926: 451–470, fig. 1.—Mortensen, 1927: 386–388.—Deichmann, 1930: 86–87.—Heding, 1940: 356, 358–360.—Djakonov, 1952: 125.—Imaoka, 1978: 377–378.—Thandar, 1992: 163–164.—Rowe, 1995: 285.—O'Loughlin, 1998: 497.—O'Loughlin, 2002: 304.

*Filithuria* Koehler and Vaney, 1905: 81–81.—Heding, 1940: 356–357 (new synonym).

*Pseudostichopus* (*Pseudostichopus*).—Heding, 1940: 357, 360.—Imaoka, 1978: 378.—Thandar, 1992: 164.

*Pseudostichopus* (*Trachostichopus*) Heding, 1940: 357, 361.—Imaoka, 1978: 380 (new synonym).

*Plicastichopus* Heding, 1940: 357 (nomen nudum).—Heding, 1942: 5–6 (new synonym).

*Peristichopus* Djakonov, 1952: 125 (new synonym).

**Type species.** *Pseudostichopus mollis* Théel, 1886 (subsequent designation by Fisher, 1907).

**Other included species.** *Pseudostichopus aemulatus* Solís-Marín and Billett, 2004; *P. echinatus* Thandar, 1992; *P. elegans* (Koehler and Vaney, 1905); *P. hyalegerus* (Sluiter, 1901); *P. mollis* Théel, 1886; *P. occultatus* Marenzeller, 1893; *P. papillatus* (Djakonov, 1952); *P. peripatus* (Sluiter, 1901); *P. profundus* Djakonov, 1952; *P. spiculiferus* (O'Loughlin, 2002); *P. tuberosus* sp. nov..

**Diagnosis.** Characters of pygal-furrowed Synallactidae (above); prominent appendages (tube feet, papillae) along the paired radii only; longitudinal muscles cylindrical, not flat,

narrowly attached to the body wall; gonad tubules not branched, arising in series along the gonoduct, not from a common base; ossicles sometimes present in tube feet and papillae; tentacle ossicles predominantly unbranched rods, rarely rods with ends intertwining and side branches fused to create mesh.

**Distribution.** Cosmopolitan; 91–5453 m.

**Remarks.** The larger radial appendages of the species of *Pseudostichopus* are frequently tapered and variably elongate, extremely so in *P. elegans* (below), and when distinctly tapered are described in this work as papillae rather than tube feet.

The monotypic genus *Filithuria* Koehler and Vaney, 1905 was established for *F. elegans* Koehler and Vaney, 1905 which is assigned here to *Pseudostichopus* and described in detail below. *F. elegans* has the diagnostic characters of *Pseudostichopus* (above), and the dorsolateral radial papillae are distinctively elongate. The dorsolateral appendages in the type species for *Pseudostichopus*, *P. mollis*, are moderately elongate and distinctly tapered, and have the appearance of papillae more than tube feet. The length of the dorsolateral papillae is an inadequate single character on which to maintain the monotypic genus *Filithuria*, which becomes a junior synonym of *Pseudostichopus*.

Heding (1940) erected the genus *Plicastichopus* citing as type species the manuscript name *Plicastichopus ingolfi*. Until he formalised the name in 1942, the genus remained a nomen nudum. O'Loughlin (2002) synonymised *P. ingolfi* Heding, 1942 with *Meseres peripatus* (Sluiter), *Plicastichopus* Heding, 1942 becoming a junior synonym of *Meseres*. *Meseres peripatus* is reassigned below to *Pseudostichopus*, *Plicastichopus* now becoming a junior synonym of *Pseudostichopus*.

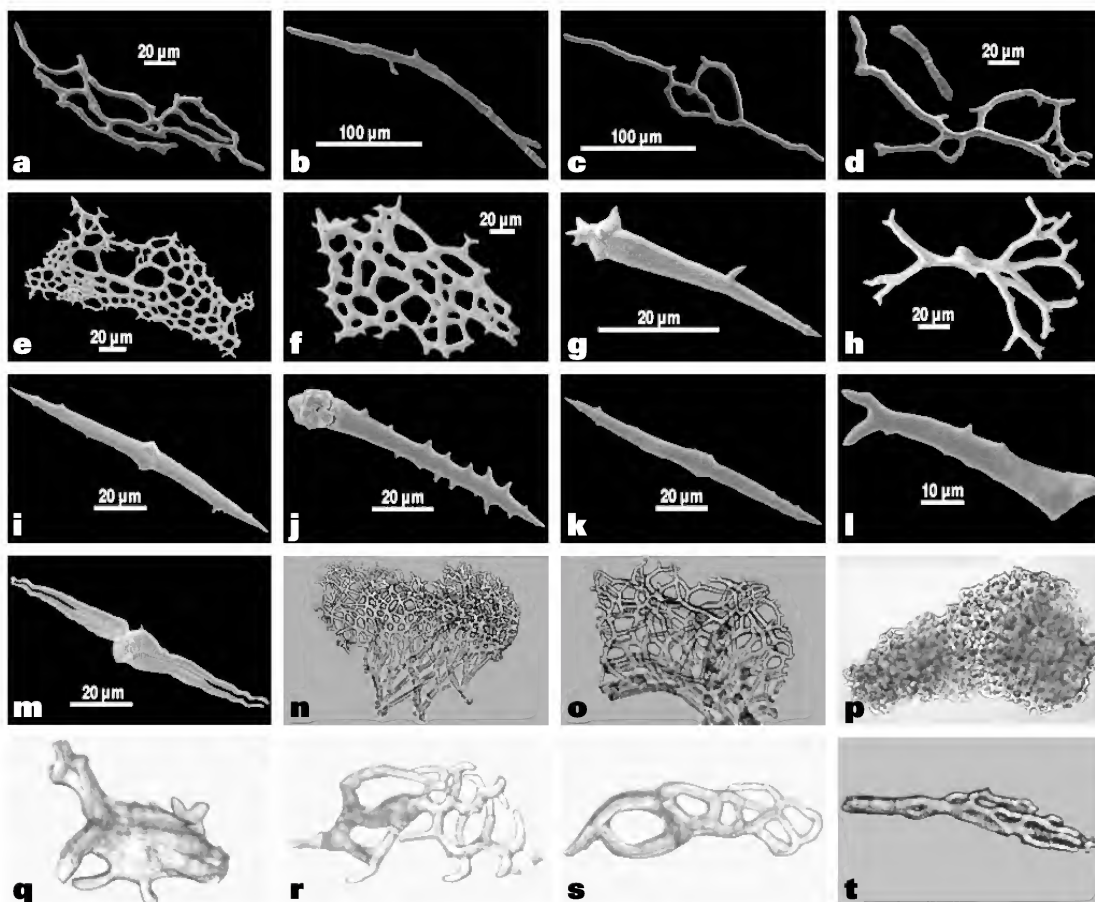


Figure 12. Gonad ossicles (SEM). a–d, *Meseres villosus* (USNM E9929). e–f, *M. translucens* sp. nov. (USNM E48652, holotype). g–h, *Pseudostichopus peripatus*, g (USNM 12198), h (USNM E48638). i–l, *P. tuberosus* sp. nov. (USNM E16721, holotype). m, *P. aemulatus* (USNM 1025525, paratype).

Posterior lobe ossicles (compound microscope). n–p, *P. hyalegerus*, n–o (NMV F80181), p (NMV F80178).

Tentacle ossicles (compound microscope). q–t, *M. ustulatus* sp. nov. (NMV F101858, paratype).

Heding (1940) erected the subgenus *Trachostichopus* (of *Pseudostichopus*), with type species *Pseudostichopus trachus* Sluiter. Rowe (1995) referred *trachus* to *Meseres* Ludwig, *Pseudostichopus* (*Trachostichopus*) becoming a junior synonym of *Meseres*. *P. trachus* is considered below to be a junior synonym of *Pseudostichopus mollis*, *Trachostichopus* now becoming a junior synonym of *Pseudostichopus*.

The monotypic genus *Peristichopus* was established for *Peristichopus papillatus* Djakonov, 1952. Djakonov (1952) characterised the genus by: cylindrical body; ventral mouth, anus; pygal furrow; small tube feet on paired radii; cylindrical longitudinal muscles; unbranched gonad tubules in two bundles; tentacles with rod ossicles, some rod ossicles perianally and in tube feet; and body wall, genital tubules, respiratory

trees lacking ossicles. Djakonov (1952) noted that *Peristichopus* was close to *Pseudostichopus*, but gave no diagnostic distinctions. *Peristichopus papillatus* is very close to *Pseudostichopus mollis*, and no justification is found here for maintaining *Peristichopus* Djakonov which is a junior synonym of *Pseudostichopus* Théel.

#### *Pseudostichopus aemulatus* Solís-Marín and Billett, 2004

Figures 11a, b, 12m

*Pseudostichopus* sp.—Billett, 1988: 196–197.—Billett et al., 2001: 325–348.

*Pseudostichopus aemulatus* Solís-Marín and Billett (in Solís-Marín et al.), 2004: 1079–1084, figs 1, 2, tables 5, 6.

**Material examined.** Paratypes. Northeast Atlantic Ocean, Porcupine Abyssal Plain, 48°45'–48°48'N, 16°36'–16°41'W, 4835–4838 m, RRS *Discovery*, stn 54901#5, 28 Apr 1999, USNM 1025525 (3).

**Description.** Up to 146 mm long; body wall thick, gelatinous, opaque, sometimes encrusted with foraminiferans and sand; distinct brim, flat ventrally, convex dorsally; body surface smooth, lacking close wrinkling with ridges and digitate projections; tapering papillae in double irregular series on dorso-lateral radii, series not widely separated, papillae typically up to 1.5 mm long, 1.0 mm diameter at base; papillae in widely separated double series ventrolaterally, dorsal to or ventral to or on brim; ossicles in tentacles and gonad; tentacle ossicles abundant, tapering rods, thick to thin, finely to bluntly spinous or smooth, with or lacking mid-rod swelling, rarely with short branches, up to 260 µm long; gonad ossicles predominantly small, thin, pointed, unbranched rods with mid-rod swelling, some with sparse blunt spines, rods up to 140 µm long.

**Colour.** Body off-white.

**Distribution.** NE Atlantic Ocean, Porcupine Abyssal Plain, 4350–4850 m (Solís-Marín et al., 2004).

**Remarks.** *P. aemulatus* is similar to *P. peripatus* (below), but is distinguished by: body wall off-white (not greyish), opaque (not semi-translucent), smooth (lacking ridges with digitate projections); dorsolateral double series of papillae not widely separated; ventrolateral double series of papillae widely separated; papillae lack ossicles; gonad ossicles predominantly unbranched pointed rods with mid-rod swelling. These characters also distinguish *P. aemulatus* from other *Pseudostichopus* species.

***Pseudostichopus echinatus* Thandar, 1992**

*Pseudostichopus* (*Pseudostichopus*) sp.—Heding, 1940: 360–361, fig. 16.

*Pseudostichopus* (*Pseudostichopus*) *echinatus* Thandar, 1992: 164–167, fig. 2.

**Description** (based on the descriptions by Heding, 1940, as *P. (Pseudostichopus)* sp., and Thandar, 1992, and on additional observations by A. Thandar, pers. comm.). Up to 65 mm long; dense dorsal and lateral encrustation of shells, globigerines, sand; subcylindrical body; 19 tentacles; scattered cover of very small tube feet, some more prominent dorsolateral tube feet evident amongst encrustations, series of ventrolateral tube feet in prominent series; longitudinal muscles cylindrical; unbranched gonad tubules in 2 series along gonoduct; ossicles in tentacles and tube feet only; tentacle ossicles irregular closely knobbed rods with some branching and perforations created by joined branches, not mesh-like, up to 300 µm long.

**Distribution.** Indian Ocean, off eastern Africa, 1°41'–28°22'S, 32°35'–41°47'E, 200–825 m.

**Remarks.** *P. echinatus* is known from the holotype (SAM A23435), a specimen discussed by Heding (1940), and a recent specimen from KwaZulu-Natal, 200 m (A. Thandar, pers. comm.). It has the diagnostic characters of *Pseudostichopus* above. Amongst *Pseudostichopus* species the distinguishing characters of *P. echinatus* are: encrusting cover of shells,

globigerines and sand; very irregular closely knobbed tentacle rod ossicles; absence of gonad ossicles.

***Pseudostichopus elegans* (Koehler and Vaney, 1905) comb. nov.**

Figures 9c, 11c, d

*Filithuria elegans* Koehler and Vaney, 1905: 81, pl. 6 figs 1, 2, pl. 12 figs 29–31.—Heding, 1940: 357, 362–363, fig. 18.

**Material examined.** NE Pacific Ocean, off Oregon, 3021 m, USNM E16815 (1); 1008097 (3); 2510 m, USNM E16505 (3); NMV F97447 (1); 2884 m, USNM E16497 (1); 2710 m, E16490 (4); NMV F97446 (1).

**Description.** Up to 145 mm long; elongate, subcylindrical, tapering anteriorly and posteriorly, flat ventrally, high convex dorsally, sometimes brim weakly developed; body wall thick, leathery, firm thin outer layer, soft thin semi-gelatinous inner layer; surface smooth dorsally and laterally, rugose ventrally; paired radii with double series of long tapering papillae, very thin distally, longest in upper dorsolateral series, up to 22 mm long, smaller in lower dorsolateral and double ventrolateral series; small tube feet all over body, up to 0.5 mm long, 0.3 mm diameter; ossicles in tentacles, papillae, tube feet; tentacle ossicles abundant tapering rods, long to short, thick to thin, with or lacking central thickening, rare short branching, spinous or smooth, up to 490 µm long; large dorsal papillae with rods similar to tentacles, some more sharply and abundantly spinous, shorter, up to 260 µm long; small papillae and tube feet with thick to thin rods, many with central swelling, bluntly spinous or smooth, short, up to 160 µm long.

**Colour.** Body violet-brown to reddish-brown to off-white; gonad tubules and respiratory trees pale brown; longitudinal muscles chocolate to reddish-brown.

**Distribution.** Bay of Bengal, off Andaman Is., 741 m (Koehler and Vaney, 1905); Indian Ocean, off Sumatra, 750 m (Heding, 1940); North-east Pacific Ocean, off Oregon, 2510–3021 m (this paper).

**Remarks.** Koehler and Vaney (1905) and Heding (1940) reported single specimens of *Filithuria elegans*. *Filithuria* Koehler and Vaney is considered above to be a junior synonym of *Pseudostichopus* Théel. The distribution of *P. elegans* is extended here from the Indian Ocean to the NE Pacific Ocean, to greater depths. Amongst *Pseudostichopus* species the distinguishing characters of *P. elegans* are: distinctly long papillae on the paired radii; numerous tapered rod ossicles in the papillae.

***Pseudostichopus hyalegerus* (Sluiter, 1901) comb. nov.**

Figures 10a, 12n–p

*Meseres hyalegerus* Sluiter, 1901a: 12.—Sluiter, 1901b: 50–51, pl. 5 figs 2–4.—Perrier, 1902: 359.

*Pseudostichopus trachus*.—Mitsukuri, 1912: 3–9, pl. 1 figs 1–5.—Ohshima, 1915: 227–228.—Mortensen, 1918: 80–81, fig. 16 (non *Pseudostichopus trachus* Sluiter, 1901).

*Pseudostichopus* (*Trachostichopus*) *tachimaruae* Imaoka, 1978: 380–382, fig. 2A–E, table 1–2 (synonymy by O'Loughlin, 2002).

*Pseudostichopus* (*Trachostichopus*) *japonensis* Imaoka, 1978: 382–384, fig. 3A–D, table 1–2.—Imaoka, 1990: 148 (synonymy by O'Loughlin, 2002).



*Pseudostichopus molpadioides* Ohshima, 1915: 228–229, pl. 8 figs 6a–c.—Heding, 1940: 353–359.—Imaoka, 1978: 384, tables 1, 2.—Imaoka, 1990: 152.—O’Loughlin, 2002: 304–305 (new synonym).

*Pseudostichopus arenosus* Ohshima, 1915: 229.—Heding, 1940: 353–359.—Imaoka, 1978: table 1–2.—O’Loughlin, 2002: 304–305 (new synonym).

**Material examined.** *Meseres hyalegerus* Sluiter. Syntypes. Indonesia, Banda Sea, 5°28’S, 132°00’E, 204 m, Siboga stn 251, ZMA V.Ech.H9499 (1); ZMA V.Ech.H2177/1 (6); ZMA V.Ech.H21772/2 (1, mounted on glass in alcohol).

*Pseudostichopus (Trachostichopus) tachimaruae* Imaoka. Holotype. Japan, W of Kyushu, near Shimo-Koshiki I., 400–450 m, T. Imaoka, 27 Oct 1976, SMBL 311. Paratypes. Type locality, date, SMBL 312 (2).

*Pseudostichopus (Trachostichopus) japonensis* Imaoka. Holotype. Japan Sea, off the Akita Prefecture, 200–300 m, S. Nishimura, 1972–1973, SMBL 313. Paratypes. Type locality and date, SMBL 314 (3).

Other material. North-west Pacific Ocean, Japan, 350–400 m, USNM 1025085 (3); 300–450 m, 1025086 (17); NMV F101861 (5); 420 m, 1071801 (1); Sagami Bay, 128–553 m, Northwest Pacific Expedition, *Albatross* stn 5092, USNM E17147 (42); NMV F101855 (5); stn 4968, USNM 1001645 (1); stn 5069, 1001646 (1); stn 5093, 1001647 (1); stn 5055, 1001648 (5); stn 5094, 1001649 (7).

Eastern Australian continental slope, Tasman Sea and Bass Strait, 293–1100 m, NMV F80171–F80175 (21), F80178 (3), F80181 (19), F80448 (1); 3300–3350 m, AM J23009 (1).

**Description.** Up to 120 mm long; typically encrusted with dense mat of predominantly sponge spicules, with shells and globigerines; frequently densely covered with tubular, thin, branched, tangled, epibiotite; body dorsoventrally depressed, subacute margin; body wall semi-gelatinous, firm, translucent to opaque, wrinkled with pits and raised protuberances all over body; short papillae on paired radii, sparse irregular double series dorsolaterally, more numerous in band ventrolaterally; papillae cylindrical at base, tapering distally, typically 2.0 mm long, 0.3 mm diameter (at base); gonad tubules predominantly unbranched, rarely singly branched, rarely bifid distally; ossicles in tentacles, papillae, pygal lobes; tentacle ossicles irregular, frequently spinous, elongate rods, branching rare, up to 340 µm long; papillae with rare irregular rods up to 100 µm long; papillae sometimes with “endplates”, very irregular perforated plates or irregular mesh of branched rods, up to 70 µm wide; pygal lobe ossicles single, large, elongate, up to 800 µm long, comprising dense perforated mesh of branched rods connected with open mesh, bluntly spinous marginally.

**Colour.** Body grey to off-white; papillae pale brown to off-white.

**Distribution.** West Pacific, Indonesia, Banda Sea, 204 m (Sluiter, 1901a); Japan, Sagami Sea, 141–564 m (Mitsukuri, 1912, as *P. trachus*); Japan Sea, south of Honshu, 128–553 m (Ohshima, 1915, as *P. trachus*); 200–300 m (Imaoka, 1978, as *P. japonensis*); Hokkaido, Shiribeshi, 714 m (Ohshima, 1915, as *P. molpadioides*), Kyushu, Koshiki Is, 781 m (Ohshima, 1915, as *P. arenosus*); 400–450 m (Imaoka, 1978, as *P. tachimaruae*); eastern Australia, Tasman Sea and Bass Strait, 293–1100 m (this work).

**Remarks.** Eight of the eleven syntypes were present (Apr 2002) in the ZMA and examined. All were taken from the same locality, and the establishment of a lectotype is not necessary.

The characters of *Meseres hyalegerus* are consistent with the diagnosis of *Pseudostichopus*, and *M. hyalegerus* is reassigned to *Pseudostichopus*.

The types of *Pseudostichopus molpadioides* Ohshima, 1915 and *P. arenosus* Ohshima, 1915 cannot be located (see Introduction). The principal characters of *Pseudostichopus molpadioides* given by Ohshima (1915) are: up to 52 mm long; cylindrical form; pygal furrow; covered by sand, foraminiferans, some sponge spicules; 20 tentacles; tube feet in double rows on paired radii, most numerous ventrolaterally, up to 2.0 mm long; unbranched gonad tubules; irregular spiny ossicles perianially, up to 200 µm long; tube feet support rods up to 120 µm long, endplates up to 140 µm wide; lacking gonad ossicles. Ohshima (1915) considered that *Pseudostichopus arenosus* closely resembled *P. molpadioides*, the two species differing only in minor differences in the form of tentacle ossicles and absence of tube feet support rods in *P. arenosus*. In this study the detection of tube foot support rods in *P. hyalegerus* was not consistent, and the differing details of tentacle ossicle form in *P. hyalegerus* fell within the variations reported by Ohshima (1915). *P. arenosus* is considered here to be a junior synonym of *P. molpadioides*. The only characters distinguishing *P. molpadioides* from *P. hyalegerus* are the typical cover of predominantly sponge spicules in the latter, and possible differing form of perianal ossicles. The drawing of a perianal ossicle for *P. molpadioides* by Ohshima (1915) is identical with a fragment of the large perianal ossicles found in *M. hyalegerus*. A variation in body cover from predominantly to only some sponge spicules is considered here to be not diagnostically adequate for distinguishing the species. *P. molpadioides* and *P. arenosus* are thus junior synonyms of *P. hyalegerus*.

O’Loughlin (2002) considered *P. tachimaruae* and *P. japonensis* to be junior synonyms of *M. hyalegerus*, based on the descriptions by Imaoka (1978). The types were examined in this work, and the pygal lobe mesh ossicles unique to *P. hyalegerus* were found in paratypes of both *P. tachimaruae* and *P. japonensis*. The synonymies are confirmed here.

Amongst *Pseudostichopus* species, the distinguishing characters of *P. hyalegerus* are: encrusting mat of sponge spicules and other attachments; ossicles in the papillae and pygal lobes.

### *Pseudostichopus mollis* Théel, 1886

Figures 1b, c, 9a, e, 10b, c, 11e, f

*Pseudostichopus mollis* Théel, 1886: 169–170, pl. 10 figs 5, 6.—Ludwig, 1898: 7.—Perrier, 1902: 337–338.—Fisher, 1907: 691.—Ekman, 1925: 5, 28–36, figs 4, 5.—Ekman, 1926: 451–470, fig. 1d.—Heding, 1940: 353–360.—Imaoka, 1978: table 1–1.—Imaoka, 1990: 148.—Gutt, 1991a: 147, 152, figs 3, 6, table 2.—Gutt, 1991b: 321, 324.—Thandar, 1992: 167.—Rowe, 1995: 285.—O’Loughlin, 2002: 304.

*Pseudostichopus trachus* Sluiter, 1901a: 15–16.—Sluiter, 1901b: 52–53, pl. 5 fig. 1, pl. 8 fig. 8.—Perrier, 1902: 337–338.—Fisher, 1907: 693.—Ekman, 1925: 32–36.—Savel’eva, 1941: 74.—Djakonov, 1952: 127, 129.—Baranova, 1957: 239.—Djakonov et al., 1958:

366.—Imaoka, 1978: 384.—Cherbonnier and Féral, 1981: 383, 385, fig. 16.

*Pseudostichopus nudus* Ohshima, 1915: 230.—Ekman, 1925: 32–36.—Heding, 1940: 353–359.—Djakonov et al., 1958: 367.—Rowe, 1995: 285 (as junior synonym of *Pseudostichopus pustulosus*; non *Pseudostichopus pustulosus* Sluiter, 1901; new synonym).

*Pseudostichopus (Trachostichopus) trachus*.—Heding, 1940: 353–362, fig. 17.—Imaoka, 1978: table 1–2.—Thandar, 1992: 166.

*Pseudostichopus (Pseudostichopus) dilatorbis* Imaoka, 1978: 378–380, 384, fig. 1 A–E, table 1–1 (part; paratypes non *P. dilatorbis*; new synonym).

*Pseudostichopus (Pseudostichopus) alatus* Imaoka, 1990: 146–148, fig. 1A–E (new synonym).

*Meseres trachus*.—Rowe, 1995: 285.—O'Loughlin, 1998: 497.—O'Loughlin, 2002: 300, 312, table 3 (new synonym).

*Pseudostichopus pustulosus*.—Rowe, 1995: 285 (non *Pseudostichopus pustulosus* Sluiter, 1901).

**Material examined.** *Pseudostichopus mollis* Théel, 1886. Lectotype (designated here). Southern Pacific Ocean, off Chile, 52°45'S, 73°46'W, 448 m, *Challenger* stn 311, BMNH 2002.293. Paralectotypes, type locality and date, 86.10.2.143 (3), 1956.10.3.6 (2); off Chile, 50°56'S, 74°14'W, 256 m, *Challenger* stn 309A, 86.10.2.142 (3); Southern Indian Ocean, off Marion I., 46°48'S, 37°49'E, 91–137 m, *Challenger* stn 144A, 86.10.2.144 (2).

*Pseudostichopus trachus* Sluiter, 1901. Lectotype (designated here). Indonesia, Ceram Sea, 1°11'S, 130°09'E, 798 m, *Siboga* stn 161, ZMA V.Ech.H2496.2 (1). Paralectotype, Timor Sea, 8°50'S, 127°02'E, 883 m, *Siboga* stn 286, V.Ech.H2496.1 (1).

*Pseudostichopus nudus* Ohshima, 1915. Neotype (designated here). North Pacific Ocean, Bering Sea, USA, Alaska, Aleutian Is, Bowers Bank, 54°33'N, 178°45'E, 1019–1068 m, RV *Albatross*, North-west Pacific Expedition, stn 4774, 4 Jun 1906, USNM E10787. Same locality and date, 1008140 (4).

*Pseudostichopus (Pseudostichopus) alatus* Imaoka, 1990. Holotype, Japan, Tosa Bay, 350 m, H. Horikawa, 30 Jan 1989, OMNH Iv1188. Paratype, Tosa Bay, 390–410 m, Iv1189 (1).

Other material. North Pacific Ocean, Bering Sea, Alaska, Bowers Bank, 1068 m, USNM E10697 (1); off southern California, W of San Nicolas I., 825 m, 32416 (19); off Oregon, 44°36'–46°01'N, 124°40'–124°45'W, 320–466 m, USNM E16503 (13); E16734–E16742 (20); E16745, E167446 (6); E16749–E16752 (9); E16886 (3); E16888 (16); E53270 (2); off San Diego, 572 m, E2042 (2); 762 m, E02035 (4); 379–636 m, E17014 (1); 914–969 m, E17016 (1); 1587 m, 32410 (3); Costa Rica, 245 m, 18269 (2).

South Pacific Ocean, south-eastern Australian continental slope, 460–1200 m, AM J16749 (1); J16836 (1); J20028 (2); J22248 (1); J22938, J22939 (3); J22943 (2); J22955 (5); J22957 (1); J22960 (7); J22964 (1); J22967–J22969 (9); J22972 (1); J22974, J22975 (6); J23218 (1); J23220 (1); J23268 (1); NMV F80176, F80177 (2), F80179, F80180 (5); TM H3111 (1); H3114 (2); W of Cape Sorrell, 972 m, H2004 (2); Tasman Sea, Lord Howe Rise, 1920 m, NMV F97692–F97694 (4); New Zealand, Campbell I., 589–594 m, USNM E48604 (2); Chatham Is, 964–1067 m, E48641 (1); Antipodes Is, 384–397 m, E48665 (7); off Chile, 960 m, 1002911 (2); Macquarie I., NMV F89907 (1); F85036 (4); 900 m, F89908 (1); Strait of Magellan, 485 m, USNM E48639 (3); 256–320 m, E48666 (25); 769–869 m, E48656 (7).

Antarctica, Palmer Archipelago, 460–500 m, USNM 1005855 (1); 460–500 m, 1008441 (2); Antarctic Peninsula, 500–670 m, 1005856 (1); 630–650 m, 1022611 (2).

**Description.** Up to 225 mm long; body rounded in transverse section, frequently flat ventrally, high convex dorsally; some-

times thick to thin, rounded, ventrolateral brim, especially anteriorly; pygal furrow sometimes barely evident in largest specimens; body wall leathery, firm, thick to thin; anterior mid-dorsal soft inconspicuous madreporite; ventrally frequently rugose, wrinkled with pockets and fine transverse ridges, folds and protuberances sometimes evident along ventrolateral margin, sometimes with raised multilobed tubercles pygally or midventrally or in lateroventral series, tubercles sometimes surmounted by tube feet, ventrum frequently encrusted with globigerines; papillae most evident dorsolaterally in sparse radial band, frequently 2 up to 4 wide, strongly tapered, somewhat whip-like, up to 5 mm long (170 mm long specimen), frequently withdrawn or lost leaving pits; double series of ventrolateral tube feet rarely externally evident; minute tube feet ventrally, rarely evident; ossicles in tentacles, tube feet, perianally; tentacle ossicles numerous to sparse, irregular rods, typically 120–240 µm long, frequently swollen mid-rod, some thin branches, rare blunt spines, branches rarely connecting to create perforations, lacking mesh ossicles, rare large irregular tuber-like ossicles, up to 380 µm long; tube feet ossicles predominantly irregular, smooth, rarely branched rods, frequently with swelling mid-rod, typically 100–130 µm long; pygal lobes with small globular mesh ossicles, difficult to detect.

**Colour.** Body, tube feet pale brown to off-white; tentacles, longitudinal muscles dark brown to brown; gonad tubules, respiratory trees pale brown.

**Distribution.** Western Antarctica, Weddell Sea, 65°19'S, 56°48'W, 400 m (Ekman, 1925); Weddell Sea, 340–470 m (Gutt, 1991); North and South Pacific Ocean, southern Indian Ocean, eastern Australian continental slope, Antarctic Ocean in Palmer Archipelago and off Antarctic Peninsula, 91–1587 m (this work).

**Remarks.** Théel (1886) listed “numerous” syntypes from *Challenger* stn 311. Six of these specimens (in three lots) were examined in the BMNH (Apr 2002), and one disintegrated specimen examined (Apr 2002) in ZMU (ZMA V.Ech.H2999). One of these specimens is designated as lectotype above. Théel (1886) also listed six specimens from stn 309A of which three were examined in the BMNH. Théel (1886) further listed two specimens from stn 144A, and both were present in the BMNH.

During an examination (Apr 2002) of holothurian types in the University of Amsterdam, a type specimen of *Pseudostichopus trachus* Sluiter was found to be registered as *Pseudostichopus pustulosus* (discussed above under *M. pustulosus*). This specimen is designated the lectotype for *P. trachus*. O'Loughlin (2002) judged material referred to *P. trachus* by Mitsukuri (1912) and Ohshima (1915) to be *M. hyalegerus*, and raised doubts about determination of material as *P. trachus* by Heding (1940), Savel'eva (1941), Baranova (1957), Djakonov et al. (1958), and Cherbonnier and Féral (1981).

Significant features of the types of *P. trachus* are: large size, up to 180 mm long (Sluiter, 1901b); slightly dorsoventrally depressed, flat ventrally, convex dorsally, pygal furrow, leathery wrinkled body wall, subacute pustulose margin with distinct small irregular protuberances; densely covered with globigerine attachments; tube feet all withdrawn, paired radial

series ventrolaterally, small ones ventrally (Sluiter 1901b), dorsal tube feet sparsely evident dorsally (Sluiter, 1901b); cylindrical longitudinal muscles ("not round in cross section" according to Sluiter, 1901b), but seen here to be round but sometimes slightly flattened); long thin unbranched gonad tubules; "teeth" on posterior margin of radial plates of ring; tentacle ossicles irregular thick rods, sometimes branched, branches sometimes fused to create perforations, smooth or with large thorny spines, sometimes with central swellings, up to 200  $\mu$ m long; tube foot ossicles short smooth tapered rods, frequently with central swelling; body wall, gonads, respiratory trees lacking ossicles. The types were taken in Indonesia at 798–883 m. In all respects, except the dorsal cover of globigerines and uncertain distribution of dorsolateral tube feet, *P. trachus* is indistinguishable from *P. mollis*. Many specimens of *P. mollis* have a dense ventral encrustation of globigerines, and quite wrinkled and pitted and ridged and pustulose ventrum and lateroventral edge. The presence of encrusting globigerines dorsally is considered to be not grounds for separating the species diagnostically. The various forms and sizes of the tentacle ossicles are noticeably similar for the *P. mollis* and *P. trachus* types, as are the teeth on the radial plates of the ring. The longitudinal muscles are cylindrical, and sometimes slightly flattened, in both species. The gonad tubules are uniquely long and thin and unbranched in both species. *P. mollis* is found on the Australian continental slope at depths similar to those of the *P. trachus* types. This study has shown that the degree to which the ventrolateral margin develops protuberances and serrations varies from strongly developed to non-existent within the same species such as in *Pseudostichopus peripatus* below. Similarly the ventrum may be relatively smooth or strongly pustulose with raised protuberances as observed here for *P. mollis*. *P. trachus* is thus judged here to be a junior synonym of *P. mollis*.

The "Type" for *P. nudus* nominated by Ohshima (1915), and given USNM Cat. No. 34150, cannot be traced (see Introduction). A neotype, selected from Ohshima's original material, is designated above. *P. nudus* has all but one of the distinguishing characters of *P. mollis*: firm, leathery body wall; potentially large sac-like form; small tapered tube feet on the paired radii; cylindrical longitudinal muscles; very long unbranched gonad tubules, in series along gonoduct; tentacles with irregular rod ossicles; tube feet with small rod ossicles with central swellings; absence of gonad, respiratory tree, posterior lobe ossicles. Ohshima (1915) distinguished *P. nudus* by a midventral band of tube feet which were each surrounded by pustular protuberances. A prominent midventral band of tube feet arising from protuberances was seen in a number of specimens in this study, but other specimens showed a range of ventral conditions intergrading with *P. mollis*. Small tube feet are present ventrally in *P. mollis*, and in some specimens become evident and in some arise from irregular swollen protuberances. *P. nudus* is also considered here to be a junior synonym of *P. mollis*.

Rowe (1995) considered *P. nudus* to be a junior synonym of *P. pustulosus*. This synonymy is rejected above (see *M. pustulosus*). Rowe (1995) identified material from off Newcastle on

the eastern Australian slope as *Pseudostichopus pustulosus*. All Australian slope material has been examined and none determined as *P. pustulosus*. Material from off Newcastle (AM J16749) was determined as *P. mollis*. Ludwig (1894) referred material to *P. mollis*, but illustrated (Ludwig, 1894, pl. 9 figs 5–9) ossicles from the genital tubules that are similar to those in the gonads of *P. peripatus* (see below). At least some of the material was not *P. mollis*, which consistently lacks gonad ossicles.

The two paratypes of *P. dilatorbis* have all the diagnostic characters of *P. mollis*, and are so assigned (see above).

The distinctive features of the two type specimens of *P. alatus* are: up to 115 mm long; pale brown to white, opaque body encrusted with sponge spicules, foraminiferans, shell, sand; 19 pale brown tentacles; tube feet on paired radii, more numerous ventrolaterally; very small tube feet ventrally; long thin unbranched gonad tubules in series along gonoduct; ossicles in tentacles only, not in gonads or tube feet; tentacle ossicles irregular rods about 150–400  $\mu$ m long, frequently with fairly large spines, rare branching. The types of *P. alatus* exhibit all of the characteristics of *P. mollis* and *P. trachus*, and these observations are confirmed by the description of Imaoka (1990). *P. alatus* is considered here to be a junior synonym of *P. mollis*.

Amongst *Pseudostichopus* species, the distinguishing characters of *P. mollis* are: leathery brown body wall; typical absence of a dense cover of globigerines or sponge spicules; distinct papillae on the paired radii; absence of gonad ossicles.

#### *Pseudostichopus occulatus* Marenzeller, 1893

*Pseudostichopus occulatus* Marenzeller, 1893a: 15–17, pl. 4 fig. 9.—Marenzeller, 1893b: 10, pl. 2 fig. 3a–c.—Perrier, 1902: 337–338.—Mortensen, 1918: 81.—Mortensen, 1927: 387–388.—Deichmann, 1930: 89–90.

*Molpadiodemas occulatus*.—Heding, 1940: 353–359.

*Meseres occulatus*.—O'Loughlin, 1998: 497.—O'Loughlin, 2002: 307, tables 1, 3.

*Material examined*. Syntypes. Mediterranean Sea, Crete, 35°4'N, 24°17'E, 1445 m, 31 Aug 1891, MNHN EcHh 3658 (2); USNM 18294 (2).

*Description*. Up to 40 mm long; encrusted with shell, sand, sponge spicule attachments; body dorsoventrally depressed, flat ventrally, low convex dorsally, acute ventrolateral margin or thin brim; body wall parchment-like, wrinkled with low reticulate ridges; appendages most evident as papillae dorsolaterally and in ventrolateral band, typically 1 mm long; ossicles in tentacles, pygal lobes, tube feet, respiratory trees; tentacle ossicles thick to thin irregular rods, some with central swellings, rare short branches, rare blunt spines, lacking mesh developments, up to 280  $\mu$ m long; pygal lobe ossicles irregular perforated plates, partly double-layered, up to 400  $\mu$ m long; tube foot ossicles smooth tapered rods with central swelling, typically 80  $\mu$ m long, "endplates" clusters of very irregular twisted branched rods or irregular perforated plates, typically 80  $\mu$ m wide; respiratory tree ossicles abundant thin, smooth, symmetrically branched, pointed rods, typically 80  $\mu$ m long.



**Colour.** Body surface appearance brown, body wall texture grey.

**Distribution.** Mediterranean Sea, 415–1445 m (Marenzeller, 1893a); North Atlantic, Spain, off Cape Finisterre, 363–510 m (Marenzeller, 1893b).

**Remarks.** *P. occultatus* has the diagnostic characters of *Pseudostichopus*, and is returned to its original combination. O'Loughlin (2002) described thin, tubular appendages covering the whole body. These are considered here to be epibiotes. Amongst *Pseudostichopus* species, the distinguishing characters of *P. occultatus* are: short, thin, smooth, distally pointed, symmetrically branched, respiratory tree ossicles; "endplate" ossicles; irregular, partly double-layered, perforated plate ossicles in the pygal lobes.

***Pseudostichopus papillatus*** (Djakonov, 1952) comb. nov.

Figures 10d, e

*Peristichopus papillatus* Djakonov, 1952: 125–127, figs 11–14.

**Material examined.** Syntypes. Russia, SE of Kamchatka, 52°45'N, 161°41'E, 4100–4200 m, 25 Jul 1946, RAS (6).

**Description.** Up to 65 mm long; torpedo-shaped body, some gravel attachments; translucent body wall; prominent small tapered papillae, arising singly on wart-like tubercles in double rows on paired radii, typically 1.5 mm long; ossicles in tentacles, papillae; tentacle ossicles unbranched thick to thin, irregular rods, some swollen centrally, rugose at ends, some bluntly spinous, up to 280 µm long; papillae ossicles irregular branching rosette-like endplates, irregular rods, some swollen centrally, some spinous, up to 260 µm long.

**Distribution.** Russia, SE of Kamchatka, 4100–4200 m.

**Remarks.** Djakonov (1952) referred this species to his new genus *Peristichopus*, which is considered above to be a junior synonym of *Pseudostichopus*. Amongst *Pseudostichopus* species, the distinguishing characters of *P. papillatus* are: the regular paired series of low tubercles and papillae on each of the paired radii; rosette-like "endplate" ossicles in papillae.

***Pseudostichopus peripatus*** (Sluiter, 1901) comb. nov.

Figures 1f, 10f–h, 11i–l, 12g, h

*Meseres peripatus* Sluiter, 1901a: 10–11.—Sluiter, 1901b: 48–49, pl. 5 fig. 5, pl. 8 fig. 7.—Perrier, 1902: 359.—Rowe, 1995: 285.

*Pseudostichopus occultatus*.—Hérouard, 1902: 14–15, pl. 2 figs 4–14 (part, illustrated; non *Pseudostichopus occultatus* Marenzeller, 1893).

*Pseudostichopus occultatus* var. *plicatus* Koehler and Vaney, 1905: 9–10, pl. 3 fig. 8, pl. 9 figs 1–3.—Heding, 1940: 353 (non *Pseudostichopus occultatus* Marenzeller, 1893).

*Pseudostichopus propinquus* Fisher, 1907: 691–693, pl. 71 fig. 3, pl. 72 fig. 2, pl. 73 fig. 3, pl. 74 fig. 1, pl. 76 fig. 3.—Imaoka, 1978: 382 (new synonym).

*Pseudostichopus aleutianus* Ohshima, 1915: 228, pl. 8 figs 5a–c.—Imaoka, 1978: 380.

*Pseudostichopus unguiculatus* Ohshima, 1915: 230–231, pl. 8 figs 7a–c.—Imaoka, 1978: 384.—Rowe, 1995: 285.

*Pseudostichopus marenzelleri* Hérouard, 1923: 25.—Mortensen, 1927: 287–288.—Deichmann, 1930: 90.

*Pseudostichopus lapidus* Hérouard, 1923: 26–28, pl. 4 fig. 5.

*Pseudostichopus (Pseudostichopus) lapidus*.—Heding, 1940: 353–360 (new synonym).

*Pseudostichopus (Pseudostichopus) marenzelleri*.—Heding, 1940: 353–359.—Imaoka, 1978: table 1–1.—Thandar, 1992: 167 (synonymy by O'Loughlin, 2002).

*Pseudostichopus (Pseudostichopus) unguiculatus*.—Heding, 1940: 353–360.—Imaoka, 1978: table 1–1.—Imaoka, 1990: 152.—Thandar, 1992: 167 (synonymy by Rowe, 1995).

*Pseudostichopus (Trachostichopus) aleutianus*.—Heding, 1940: 353–359.—Imaoka, 1978, table 1–2 (synonymy by O'Loughlin 2002).

*Plicastichopus plicatus*.—Heding, 1940: 354–359.—Heding, 1942: 6. (synonymy by O'Loughlin, 2002).

*Pseudostichopus (Trachostichopus) propinquus*.—Heding, 1940: 357.—Imaoka, 1978: table 1–1.—Imaoka, 1990: 148, 152.

*Plicastichopus ingolfi* Heding, 1942: 5–6, figs 4–5, pl. 1 figs 4–5.

*Pseudostichopus (Trachostichopus) tuberculatus* Imaoka, 1990: 149–152, pl. p. 149, fig. P. 15. (synonymy by O'Loughlin, 2002).

*Meseres ingolfi*.—Rowe, 1995: 285 (synonymy by O'Loughlin, 2002).

*Meseres propinquus*.—O'Loughlin, 2002: 309.

**Material examined.** *Meseres peripatus* Sluiter, 1901. Lectotype (designated here). Indonesia, Flores Sea, 7°24'S, 118°15'E, 794 m, *Siboga* stn 45, ZMA V.Ech.H9500. Paralectotypes. Type locality and date, ZMA V.Ech.H1048 (2); Maluka Sea, 1°59'N, 125°01'E, 1200 m, *Siboga* stn 122, ZMA V.Ech.H1049 (1); Banda Sea, 5°41'S, 120°46'E, 1158 m, *Siboga* stn 211, ZMA V.Ech.H1050 (2).

*Pseudostichopus propinquus* Fisher, 1907. Holotype. Hawaiian Is, 21°11'N, 156°35'W, 518–519 m, USNM 21217.

*Pseudostichopus lapidus* Hérouard, 1923. Syntypes. North Atlantic Ocean, off the Azores, 4020 m, Monaco stn 527, 1895, MOM (3) (examination by M. Bruni, pers. comm., MOM).

*Pseudostichopus (Trachostichopus) tuberculatus* Imaoka, 1990. Holotype. Japan, Tosa Bay, 660–700 m, H. Horikawa, 23 May 1989, OMNH Iv1190.

*Pseudostichopus unguiculatus* Ohshima, 1915. Syntypes. North Pacific Ocean, off Japan, 1058–1680 m, *Albatross* stns 4960, 5083, 5084, USNM 34151 (2), E24543 (1), E24544 (1).

Other material. Pacific Ocean, Tasman Sea, eastern Australia continental slope, 823–1750 m, AM J20026, J20027 (3); J23219 (1); J23267 (2); J22980 (9); NMV F80449, F80450 (3); F90070 (2); Philippines, 878 m, USNM E48764 (2); est. 1300 m, E48770 (2); off Thailand, 370 m, 1017465 (7); off Oregon, 1646 m, E48586 (3); 411 m, E17035 (2); 1946 m, E1972 (29); Mexico, 1608 m, 32389 (1); 2014 m, 32391 (2); Costa Rica, 1789 m, 18267 (1); Peru-Chile Trench, 3500 m, E53272 (1); NMV F101841 (1); Galapagos Is, 2418 m, USNM 18272 (4); 1158 m, E949 (1); 3667 m, 1008450 (1); 1008457 (2); South-west Pacific Basin, 3386–3422 m, E49306 (1); South-east Pacific Basin, N of Amundsen Sea, 4978–5043 m, E48660 (5); 4709 m, E48590 (1); 4682 m, 1022459 (1); 4575–4813 m, E48629 (1); W Balleny Is, 2836–2864 m, E48632 (2); off Victoria Land, 3459–3492 m, E48624 (2); 566–569 m, 1022604 (2); Ross Sea, 3495–3514 m, 1008176 (1).

North Atlantic Ocean, off Florida, 931m, USNM E1990 (1); off Massachusetts, 3235 m, 12198 (1); 3682 m, E53743 (1); off South Carolina, 1337 m, E2581 (2); Bahamas, 4763–4803, 1021900 (1); 4578–4778 m, 1021902 (1); 4783–4823 m, 1021901 (1); Caribbean Sea, Venezuelan Basin, 3428–3476 m, E38794 (2); 3411–3459 m, E38796 (1).

Weddell Sea, 1025–1153 m, USNM E48573 (1).

South Atlantic Ocean, Scotia Sea, 52°00'–62°30'S, 14°54'–60°40'W, 267–5453 m, USNM E48572 (1); E48574–E48577 (15); E48581 (1); E48585 (9); E48587, E48588 (2); E48592 (1); E48596 (6); E48599 (2); E48602, E48603 (5); E48607, E48608 (5); E48628 (2); NMV

F101840 (1); USNM E48638 (45); E48648 (23); NMV F101839 (5); USNM E49241 (5); E49255 (10); E49325, E49326 (7); E49348, E49349 (2); E49351 (1); E49444, E49445 (3); 1008141 (6); NMV F101838 (3); USNM 1008159, 1008160 (7); 1008166 (5); 1008297 (4); 1022445 (2); 1022463 (3).

Antarctic Ocean, South Orkney Is, 3250–3285 m, USNM 1008177 (3); 1228–1400 m, E49393 (1); South Shetland Is, 662–1120 m, E48570 (1); 884–935 m, E48610 (7); 213–311 m, E49350 (1); South Sandwich Trench, 5350 m, USNM 1071584 (2); Palmer Peninsula, 134 m, E49259 (1).

**Description.** Up to 140 mm long; form of body variable, typically with encrusting globigerine or grit attachments; body elongate, slightly tapered anteriorly and posteriorly, depressed to varying degrees dorsoventrally, flat ventrally, typically low convex dorsally; body wall firm, leathery, thick to thin, semi-gelatinous, frequently with deep transverse grooves and ridges, frequently wrinkled with low reticulate ridges surmounted by small digitate projections, frequently pitted with withdrawn very small interradiate tube feet; ventrolateral margin acute to subacute, rounded, variably serrated by the transverse body folds and irregular transverse creases; ventrolateral margin variable from rounded, to mammiform, to rounded protuberances surmounted by elongate to multiple-knobbed extensions, to knobbed domes further surmounted by smaller knobs or small tube feet or larger radial tube feet; larger tube feet surmount double radial series of mammiform bases, not present midventrally, mammiform base and papilla typically 2.0 mm long; ossicles in tentacles and gonad, larger papillae; tentacle ossicles abundant large irregular rods, thick to thin, terminally tapered, frequently with central swelling, sometimes swollen distally, sometimes with small terminal knobs, sometimes bluntly spinous, sometimes branched along rod with branches closed to create perforations, rods up to 360 µm long; papillae with spinous to smooth rods, frequently with central swelling, up to 160 µm long; “endplates” sometimes detected in papillae as perforated plates with mesh collar or tangled mesh of joined irregular rods, up to 340 µm diameter; gonad ossicles frequently present, abundant, typically small predominantly slender tapering rods with small central hub, spinous to smooth, unbranched or Y- or X-shaped, sometimes irregular thick variably spinous branched rods, up to 200 µm long.

**Colour.** Body grey to off-white, to residual pale reddish-brown on some small specimens, sometimes semi-translucent; radial tube feet brown, smaller tube feet off-white.

**Distribution.** Indo-Pacific Region, North and South Pacific Ocean, North and South Atlantic Ocean, Scotia Sea, Antarctic Ocean, Ross Sea, Weddell Sea; 134–5453 m.

**Remarks.** Seven syntypes of *Meseres peripatus* Sluiter, 1901 are listed (ZMA E1050) by Jangoux (1991). Only two were present when the syntypes were examined (April 2002). *M. peripatus* has the diagnostic characters of *Pseudostichopus* detailed above, and is reassigned.

The description of *P. propinquus* Fisher, 1907 referred to: thin translucent body wall, with some foraminiferan attachment; distinct thickened lateroventral margin, with mammi-

form tubercles surmounted by tube feet; paired radii with tube feet; round longitudinal muscles; unbranched gonad tubules; gonad with fine branched sometimes spinous rod ossicles, up to about 200 µm long; respiratory tree ossicles similar to gonad. All of these characters accord with the diagnosis of *Pseudostichopus* above, and *propinquus* is returned to its original combination. All of the features of *P. propinquus*, except the presence of respiratory tree ossicles, are diagnostic features of *Pseudostichopus peripatus*. Fisher (1907) referred to two specimens. The holotype is in very poor condition, and respiratory tree ossicles could not be confirmed. The second specimen was not located. If gonad-type ossicles were found in the respiratory trees of material otherwise conspecific with *P. peripatus*, this would be judged to be an individual variation rather than a basis for a separate species. *P. propinquus* is considered here to be a junior synonym of *P. peripatus*. Rowe (1995) made *P. propinquus* a junior synonym of *P. pustulosus* Sluiter, 1901. This synonymy is rejected. *P. propinquus* has the diagnostic characters of *Pseudostichopus*, and *P. pustulosus* those of *Molpadiodemas* (above).

Based on the description by Hérouard (1923), on observations communicated by M. Bruni (MOM), and on photographs by Francisco Solís-Marín (UNAM) of a tentacle ossicles slide prepared by Gustav Cherbonnier (MNHN box 108 slide 45), the characters of *P. lapidus* are: up to 15 mm long; pygal furrow; encrusting cover of foraminiferans, sand, stones; tube feet on paired radii, small to absent on midventral radius; longitudinal muscles narrow; gonad tubules unbranched; ossicles in tentacles only, lacking in body wall and internal organs; tentacle ossicles predominantly rods without branches and associated mesh. Although gonad ossicles have not been detected, *P. lapidus* has the distinctive characters of *Pseudostichopus peripatus* and it is judged here to be a junior synonym.

O’Loughlin (2002) considered *P. marenzelleri* to be a junior synonym of *P. peripatus*, based on the description and figures by Hérouard (1923). Based on the additional description by M. Bruni (MOM, pers. comm.) of cylindrical longitudinal muscles and unbranched gonad tubules, the synonymy is confirmed here. O’Loughlin (2002) considered *P. tuberculatus* to be a junior synonym of *P. peripatus*, based on the photograph and description in Imaoka (1990). Following an examination of the holotype the synonymy is confirmed.

The considerable variety in ossicle and body form, and cosmopolitan distribution and depth range, suggested to us that there are probably more than one species involved. We were unable to recognize discrete diagnostic characters on which to distinguish further species.

The distribution summary by O’Loughlin (2002) indicated an Indo-Pacific and North Atlantic distribution for *P. peripatus*. Data above extend the distribution to the eastern Pacific, western and southern Atlantic, and Antarctic Oceans, and to significantly shallower and greater depths.

Amongst *Pseudostichopus* species, the distinguishing characters of *P. peripatus* are: dorsoventrally depressed body, with strong wrinkling and transverse creases creating a serrated ventrolateral margin; typical encrusting cover of globigerines or rounded grit attachments, not sponge spicules; rods of various forms in gonads, no mesh ossicles.

***Pseudostichopus profundus* Djakonov, 1952**

*Pseudostichopus profundus* Djakonov, 1952: 127–129, figs 15–18.

**Material examined.** Syntype (RAS). Russia, SE of Kamchatka, 52°45'N, 161°41'E, 4100–4200 m, 25 Jul 1946.

**Description.** Up to 56 mm long; body cylindrical; body wall thick, opaque, soft; few sand grain attachments; very small tube feet unevenly distributed all over body, lengths variable, largest anteriorly and posteriorly, fewest mid-dorsally and mid-ventrally; 20 tentacles; radial plates of calcareous ring lacking "teeth"; longitudinal muscles cylindrical; gonad tubules unbranched; tentacle ossicles thick, broad, bent, irregular, variably perforated, somewhat mesh-like, typically 200 µm long; tube feet ossicles variable from irregular rods, to knots, to irregular curved mesh-like narrow plates, up to 180 µm long; posterior lobes with rare unbranched rods, irregular ends, up to 0.17 mm long; gonad and respiratory trees with small, smooth, sparse rod fragments.

**Colour.** Body and tube feet brown to grey.

**Distribution.** Russia, SE of Kamchatka, 4100–4200 m.

**Remarks.** The description above is based on Djakonov (1952). The syntype that was examined here was 27 mm long, and very soft. The longitudinal muscles were rounded laterally, but broadly attached to the body wall and not cylindrical, and are considered here to be flat. No gonad was found. The pygal tube feet were soft, cylindrical, and typically 0.3 mm long, 0.15 mm diameter. No ossicles were found in the tube feet. The absence of ossicles in the tube feet, and flat longitudinal muscles, suggest that the syntype examined here is not conspecific with *P. profundus* as described. Djakonov (1952) described very small, smooth rods in genital tubules and respiratory trees. We judge these to be probably artefacts and not ossicles, since such very small fragmentary rods are frequently present in gonad and respiratory tree preparations.

Reference by Djakonov (1952) to cylindrical longitudinal muscles and unbranched gonad tubules indicate an appropriate assignment of the species to *Pseudostichopus*. But the flat longitudinal muscles, and absence of prominent tube feet on the paired radii, indicate that the syntype examined here belongs in *Molpadiodemus*. The characters of the species, and generic assignment, remain unresolved.

Amongst *Pseudostichopus* species the unique character of *P. profundus* (as described by Djakonov) is the presence of curved mesh-like narrow plates in the tube feet.

***Pseudostichopus spiculiferus* (O'Loughlin, 2002) comb. nov.**

Figure 1g

*Pseudostichopus* sp. MoV 2068.—O'Loughlin et al., 1994: 253–255.

*Meseres spiculiferus* O'Loughlin, 2002: 309–312, figs 1a–f, 2a–d, tables 1–3.

**Material examined.** (See O'Loughlin, 2002). Antarctic Ocean, Weddell Sea, 1554 m, USNM 49279 (1); Antarctic Peninsula, 370–375 m, E48582 (1); 246–270 m, E49242 (2); 326 m, 49258 (2); 460–500 m, E49472 (4); Ross Sea, 73°58'–78°23'S, 168°50'E–161°57'W, 364–728 m, E48598 (2); E48643 (2); E49268, E49269 (7);

1005124 (1); E49287 (2); E49354 (1); E49358 (2); 485–490 m, 1005121 (4); 1005123 (3); New Zealand, Antipodes Is, 2010–2100 m, 1005113 (1).

**Description.** Up to 105 mm long; body typically encrusted with sponge spicules, sometimes globigerines; body flat ventrally, convex dorsally; lateroventral margin subacute, some reticulate ridges with small digitate projections, lacking prominent ventrolateral projections; irregular double rows of tube feet dorsolaterally, larger along ventrolateral margin in band up to 5 irregular rows wide and continuous around anterior body, sometimes contiguous, up to 3.0 mm long, 0.8 mm diameter; ossicles in tentacles, tube feet and gonad; tentacle ossicles thick to thin, curved to straight irregular rods, frequently swollen mid-rod, rarely swollen terminally, rarely branched, rarely bluntly spinous, up to 320 µm long; tube feet with rods distally, same form as tentacle rods, up to 200 µm long; "end-plates" of close cluster of irregular rods, up to 130 µm wide; gonad ossicles abundant smooth rods, tapered to points at ends, variable shape, frequently with central swelling, X- or Y-shaped or complex multiple branching, branches sometimes joined to create large perforations, ossicles frequently 120 µm long, up to 300 µm long.

**Colour.** Body off-white or grey or grey-brown; tube feet off-white to reddish-brown.

**Distribution.** Eastern Antarctica, off Wilkes, MacRobertson, Enderby Lands, 177–695 m (O'Loughlin, 2002); Ross Sea, 364–728 m; Antarctic Peninsula, 246–500 m; Weddell Sea, 1554 m; New Zealand, Antipodes Is, 2100 m.

**Remarks.** *Meseres spiculiferus* has the diagnostic characters of *Pseudostichopus* above, and is reassigned. The above data extend the distribution of O'Loughlin (2002) from eastern Antarctica to the Weddell Sea and New Zealand Antipodes Is, and depth to 2100 m. Amongst *Pseudostichopus* species, the distinguishing characteristics of *P. spiculiferus* are: dense cover of sponge spicules; absence of large pygal lobe ossicles; lateral band of tube feet; complex branching gonad ossicles.

***Pseudostichopus tuberosus* sp. nov.**

Figures 9b, f, 10i, 11g, h, 12i–l

**Material examined.** Holotype. North Pacific Ocean, off Oregon, 45°43'N, 125°13'W, 1920 m, *Commando*, 28 May 1964, USNM E16721.

Paratypes. Holotype locality and date, USNM 1008333 (1); NMV F101864 (1).

Other material. North Pacific Ocean, off southern California, 32°33'N, 118°04'W, 1937 m, USNM E17015 (1).

**Description.** Up to 140 mm long; body wall leathery, thin, firm; body flat ventrally, convex dorsally; prominent single series of ventrolateral protuberances ("warts"), irregularly rounded, typically 2.0 mm wide, domed, soft and thin-walled, or firm and flat, not surmounted by papillae, ventral to series of ventrolateral papillae; body transversely creased and wrinkled ventrally, sometimes dorsally, abundant grit attachments, ventrolateral margin with indentations and lobes created by transverse

creases; irregular double rows of tapering papillae on both paired radii, up to 2.0 mm long; minute tube feet all over body, up to 0.2 mm long; ossicles in tentacles and gonad; tentacle ossicles abundant, predominantly small thick to thin curved rods, bluntly to finely spinous or smooth, swelling mid-rod sometimes, rare short branches, rods up to 340 µm long; gonad ossicles abundant, small unbranched rods, tapering to pointed ends, slightly spinous to smooth, typically with central swelling, up to 140 µm long.

**Colour.** Body, tube feet and protuberances off-white.

**Etymology.** From the Latin *tuberosus* ("full of lumps or protuberances"), referring to the distinct large protuberances along each ventrolateral margin.

**Distribution.** North-eastern Pacific Ocean, off Oregon and southern California, 1920–1937 m.

**Remarks.** The ventrolateral protuberances are wart-like ("fungiform papillae"), and resemble similar features in *Bathyplores moseleyi*. Amongst *Pseudostichopus* species the distinguishing characters of *P. tuberosus* are: ventrolateral series of wart-like protuberances; presence of small unbranched tapered rods in the gonad.

### Incertae Sedis

#### *Meseres* Ludwig, 1894

*Meseres* Ludwig, 1894: 34, 36, 38.—Perrier, 1902: 359.—Rowe, 1995: 284–285.—O'Loughlin, 1998: 497.—O'Loughlin, 2002: 303–305.

**Type species.** *Meseres macdonaldi* Ludwig, 1894 (monotypy).

**Diagnosis** (emended from O'Loughlin, 2002). Up to 30 mm long; completely lacking ossicles; thin translucent body wall; body rounded anteriorly, posteriorly; mouth, anus ventral; lacking pygal furrow; ventrolateral margin with series of pyramidal protuberances surmounted by typically 3 digitate projections / (? tube feet); close body cover of small papillae / (? tube feet) and thin tubular appendages (probably epibiotic); 15 small shield-shaped tentacles; lacking tentacle ampullae; five small radial and five interradial plates in ring; longitudinal muscles undivided; unbranched gonad tubules on each side of dorsal mesentery; respiratory tree comprising two thin-walled tubes with sacs.

**Material examined.** *Meseres macdonaldi* Ludwig, 1894. Lectotype (designated here). Pacific Ocean, off Costa Rica, Cocos I., 5°56'N, 85°10'W, 2149 m, RV *Albatross* stn 3362, 26 Feb 1891, USNM 30501 (1). Paralectotypes. Pacific Ocean, off Colombia, Malpelo I., 4°3'N, 81°31'W, 1644 m, RV *Albatross* stn 3380, 5 Mar 1891, USNM 18190 (5 now unrecognisable specimens).

**Remarks.** The diagnosis of *Meseres* by O'Loughlin (2002) was based on the species assigned at that time to *Meseres*, and not exclusively on the type species *M. macdonaldi*. The emended diagnosis is based solely on the description of the type material by Ludwig (1894), and some observations on the remaining type material. The syntypes of *M. macdonaldi* were taken off Costa Rica at 2149 m (USNM 30501 (1)), and off Colombia at

1644 m (USNM 18190 (5)). All are in very poor condition, but a single syntype (USNM 30501) retains some recognisable tissue and body parts. For the purpose of having a precise type locality for this type species of *Meseres*, and some specific tissue for possible molecular analysis, the syntype registered alone is designated here as lectotype.

The characters of *M. macdonaldi* were not illustrated by Ludwig (1894), and all of the type material is in an advanced state of decomposition. Whether the body was covered with tube feet or papillae remains subjective. The upper limit of 15 tentacles (in this study Synallactidae species 30 mm long have more than 15 tentacles), and complete absence of ossicles, indicate that *Meseres* does not belong in the Synallactidae. *Meseres* has most of the characters of the Gephyrothuriidae as re-diagnosed by O'Loughlin (1998), with the exception of digitate tentacles. Ludwig (1894) described small shield-shaped tentacles, but there is no evidence as to what precise form they took. It is relevant to note that one of the two species of the Gephyrothuriidae reviewed by O'Loughlin (1998), *Hadalothuria wolffi* Hansen, had ventrolateral protuberances surmounted by rudimentary (?) tube feet. This feature appears to be shared with *M. macdonaldi*. The description of shield-shaped tentacles is an obstacle to referring the genus to the Gephyrothuriidae and *Meseres*, as exemplified by its type species, is treated here as incertae sedis.

Sluiter (1901) and O'Loughlin (1998, 2002) referred species to *Meseres* principally on the basis of a distinctive ventrolateral margin, and Rowe (1995) on the basis of "gonads in two discrete bunches of divided or undivided tubules, one on each side of the dorsal mesentery". All of these species referred to *Meseres* had 18–20 tentacles, a distinct pygal furrow, and tentacle ossicles, and are hence not congeneric with *M. macdonaldi*. Except for the type species *M. macdonaldi*, and *Meseres* (?) *torvus* (Théel, 1886), all species previously referred to *Meseres* are reassigned above to *Molpadiodemas* Heding or *Pseudostichopus* Théel. O'Loughlin (2002) listed *Molpadiodemas* Heding, 1935, *Trachostichopus* Heding, 1940 and *Plicastichopus* Heding 1940 as junior synonyms of *Meseres* Ludwig, 1894. These three genera are removed from the synonymy, and are discussed under *Molpadiodemas* and *Pseudostichopus* above.

O'Loughlin (2002) referred *Stichopus* (?) *torvus* Théel, 1886 to *Meseres*, based on the original description and the comparison with *Meseres macdonaldi* by Ludwig (1894). The single type specimen was collected in the South Pacific Ocean off Chile at 2516 m. A subsequent examination (Apr 2002) of the type revealed the following: strongly contracted, 160 mm long (210 mm in Théel 1886); cylindrical; irregular double rows of large tube feet on paired radii; dorsal and lateral surfaces covered with long conical papillae of varying sizes, largest ventrolaterally, rare branching; small pygal furrow present as a split above anus (possible artefact); longitudinal muscles round, deeply split (probable artefact); gonad tubules short, sac-like, branched; ossicles not detected in body wall, tentacles, papillae, tube feet, gonad, or respiratory trees. The calcareous ring was not *Pseudostichopus*-like. These characters have little affinity with *Molpadiodemas* Heding or *Pseudostichopus* Théel, and *torvus* is referred back to the original combination *Stichopus* (?) *torvus*.

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## A new asterinid genus from the Indo-West Pacific region, including five new species (Echinodermata: Asteroidea: Asterinidae)

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### Abstract

O'Loughlin, P. M., and Rowe, F.W.E. 2005. A new asterinid genus from the Indo-West Pacific region, including five new species (Echinodermata: Asteroidea: Asterinidae). *Memoirs of Museum Victoria* 62(2): 181–189.

A new genus of asterinid asteroid, *Ailsastra* gen. nov., and five new species, *Ailsastra achituvi*, sp. nov., *A. amezianeae*, sp. nov., *A. booneni* sp. nov., *A. eleaumei* sp. nov., *A. paulayi* sp. nov. (type species), are described from the Indo-West Pacific. *Asterina heteractis* H.L. Clark, 1938 is reassigned from *Aquilonastra* O'Loughlin, 2004 to *Ailsastra* gen. nov. The external morphological characters distinguishing *Ailsastra* from other genera of Asterinidae are the distinctively small oral plates and the variably sunken regular carinal series of plates. Internally, superambulacral and superactinal plates, where investigated, are known to be lacking in three species, including the type species. A key to the six species and a distribution map of type localities are provided.

### Keywords

Echinodermata, Asteroidea, Asterinidae, *Ailsastra*, new genus, new species, taxonomy

### Introduction

The Asterinidae have undergone three major revisions (Verrill, 1913; A.M. Clark, 1983; O'Loughlin and Waters, 2004). The most recent included for the first time a combination of morphological and (limited) molecular analyses. This resulted in the reassessment and rationalisation of some established genera, the description of four new genera (bringing the total to 21), and the inclusion of 103 valid species in the family.

Rowe and Richmond (2004) found, in the course of identifying specimens of two species of '*Asterina*' (= *Aquilonastra* O'Loughlin, 2004) from Rodrigues Island in the south-western Indian Ocean, that a problem lay in determining the correct identification of *Aquilonastra burtoni* (Gray, 1840) and the differentiation of supposedly conspecific species included in its synonymy. We have widened their work and undertaken a comparative and systematic study of Indo-West Pacific asterinid taxa.

In the process of solving this problem, additional new material became available from Drs Chantal Conand (La Réunion Island), Gustav Paulay (Indo-West Pacific), Matthew Richmond (western Indian Ocean), and Yves Samyn (south-eastern Africa). Loans of material (including type specimens) have been made by Muséum National d'Histoire Naturelle, Paris, The Natural History Museum, London, South African

Museum, Cape Town, Australian Museum, Sydney, Museum of Comparative Zoology, Harvard University, Massachusetts, The Hebrew University of Jerusalem, and Tel-Aviv University. The availability of this abundant material for comparative use has led to the recognition of yet further, numerous, new asterinid taxa that require description, and has allowed a review of some past, published determinations.

Amongst the new taxa it became apparent that both morphological and molecular (Jon Waters, pers. comm.; paper in preparation) evidence supported the recognition of a new, wide-spread, Indo-West Pacific genus of small, stellate asterinids with regular carinal series and small oral plates. Included in this genus are the eastern Australian species *Asterina heteractis* H.L. Clark, 1938 and five new species, extending in range from the Red Sea and western Indian Ocean to Indonesian waters. This paper includes descriptions of these taxa, and foreshadows an anticipated series on further Indo-West Pacific Asterinidae. The number of taxa included in the family now rises to 22 genera and 108 species.

Terminology follows O'Loughlin and Waters (2004). R/r values are given with the recognition that they vary within a species on the same specimen, amongst specimens, and with size of specimen. Abbreviations for institutions are: AM, Australian Museum, Sydney; MNHN, Muséum National d'Histoire Naturelle, Paris; NHM, The Natural History

Museum, London; NMV, Museum Victoria, Melbourne, Australia; UF, University of Florida, USA; MCZ, Museum of Comparative Zoology, Harvard University, Massachusetts, USA. Photographs were made with a Leica MZ16 stereomicroscope, DC300 Leica digital camera, and "Auto-Montage" software for composition of images.

## Asterinidae Gray, 1840

### *Ailsastra* gen. nov.

Figure 1

*Type species. Ailsastra paulayi* sp. nov.

*Other included species. Ailsastra achituvu* sp. nov.; *A. amezianae* sp. nov.; *A. booneni* sp. nov.; *A. eleaumei* sp. nov.; *Asterina heteractis* H.L. Clark, 1938.

**Diagnosis.** Small, stellate asterinids, up to  $R = 16$  mm; rays predominantly 5; one species fissiparous (5–7 rays); interradial margin incurved, rays discrete, broad to narrow at base, short to long, rounded distally; flat actinally, convex abactinally, inferomarginal plates project to form acute ventrolateral margin; disc distinctly to irregularly defined; carinal series of plates present for most of ray, doubly papulate with 2 longitudinal series of large papulae for most of ray, each plate with rounded anterior projection; carinal plates imbricated by adcarinal plates on both sides, forming characteristic 'sunken' series; other abactinal plates closely imbricate, not notched, arched over papular space more than indented proximally for papula; lacking secondary plates; papulae on rays single per papular space, large, in longitudinal series; spinelets glassy, thick to thin, conical or sacciform or subsacciform, pointed or splay-pointed, in clusters or single or double series across proximal plates, sometimes in round or oval bowl-shaped series on plate; lacking pedicellariae with differentiated valves; plates with prominent glassy convexities; superomarginal and inferomarginal plates in regular series; actinal interradial plates in predominantly oblique series; oral plates distinctively small, constricted distally (pair with form of short-handled, smooth-headed mace or club); oral spines up to 6, series incurved distally; suboral spines variably present, if present in continuous series with distal oral spines; lacking superambulacral and superactinal plates in type species and two other investigated species.

**Distribution.** Lord Howe I., NE Australia, Sulawesi I., Sudanese Red Sea, Mauritius, NW Madagascar; rock and coral; 0–16 m.

**Etymology.** From *Ailsa* with the Latin *astrum* (star), in recognition of the substantial contribution by Ailsa Clark to seastar systematics (feminine).

**Remarks.** Superambulacral and superactinal plates are absent from the type species *A. paulayi*, and *A. amezianae* and *A. eleaumei*. The remaining three species (which have not been dissected) have the other generic characters of *Ailsastra*, and it is anticipated that they too lack these internal plates. *Ailsastra* shares the lack of superambulacral and superactinal plates with seven other genera currently included in the Asterinidae:

*Asterina*, *Asterinides*, *Kampylaster*, *Meridiastra*, *Pseudasterina*, *Pseudopatiria* and *Tremaster* (see O'Loughlin and Waters, 2004). However, the form of the oral plates and arrangement of the carinal series of plates distinguish *Ailsastra*, morphologically, from these and all other genera in the family. The morphological justification for recognising the new genus is supported by limited molecular data that places the two specimens of the type-species *A. paulayi* sp. nov. (see below) in a highly divergent but strongly monophyletic clade within a molecular phylogeny of Asterinidae (Jon Waters, pers. comm.; paper in preparation).

### Key to species of *Ailsastra*

1. Rays 5–7; more than 1 madreporite; fissiparous ..... *A. heteractis*  
— Rays predominantly 5; single madreporite; not fissiparous ..... 2
2. Integument obscures abactinal and actinal plates; lacking superomarginal spinelets; proximal actinal large pyramidal spines present ..... *A. booneni*  
— Abactinal and actinal plates not obscured by integument; superomarginal spinelets present; lacking proximal actinal large pyramidal spines ..... 3
3. Rays narrow at base,  $R/r > 2.5$ , digitiform; spinelets up to 0.25 mm long ..... *A. paulayi*  
— Rays broad at base,  $R/r < 2.0$ , not digitiform; spinelets not longer than 0.20 mm ..... 4
4. Form subpentagonal; up to 8 longitudinal series of papulae across mid-rays; spinelets up to 0.10 mm long ..... *A. amezianae*  
— Rays discrete, form not subpentagonal; 6 longitudinal series of papulae across mid-rays; some spinelets more than 0.10 mm long ..... 5
5. Proximal abactinal spinelets frequently in bowl-shaped arrangement ..... *A. eleaumei*  
— Proximal abactinal spinelets never in bowl-shaped arrangement ..... *A. achituvu*

### *Ailsastra achituvu* sp. nov.

Figures 1, 2a, 3a, 4a–c

*Asterina burtoni*.—Clark and Rowe, 1971: 70, table 1 (part: specimen 1951.5.7.12) (non *Asterina burtoni* Gray, 1840).

**Material examined.** Holotype (in alcohol). Sudanese Red Sea, Khor Inkeifail, on coral, *Manihine* Collections, 29 Dec 1950, NHM 1951.5.7.12.

**Diagnosis.** *Ailsastra* with, at  $R = 10$  mm, discrete rays, medium length, wide at base, strongly tapered, rounded distally,  $R/r$  about 1.9; carinal series of plates narrowly visible, below adcarinal plates; 6 longitudinal series of papulae across mid-ray; spinelets splay-pointed, subsacciform to conical, up to 0.15 mm long; inferomarginal spinelets twice the length of superomarginal spinelets; up to 6 interradial actinal spines per plate.

**Description.** 5 rays,  $R = 10$  mm; integument evident; rays discrete, wide at base, tapered, rounded distally,  $R/r$  about 1.9; single

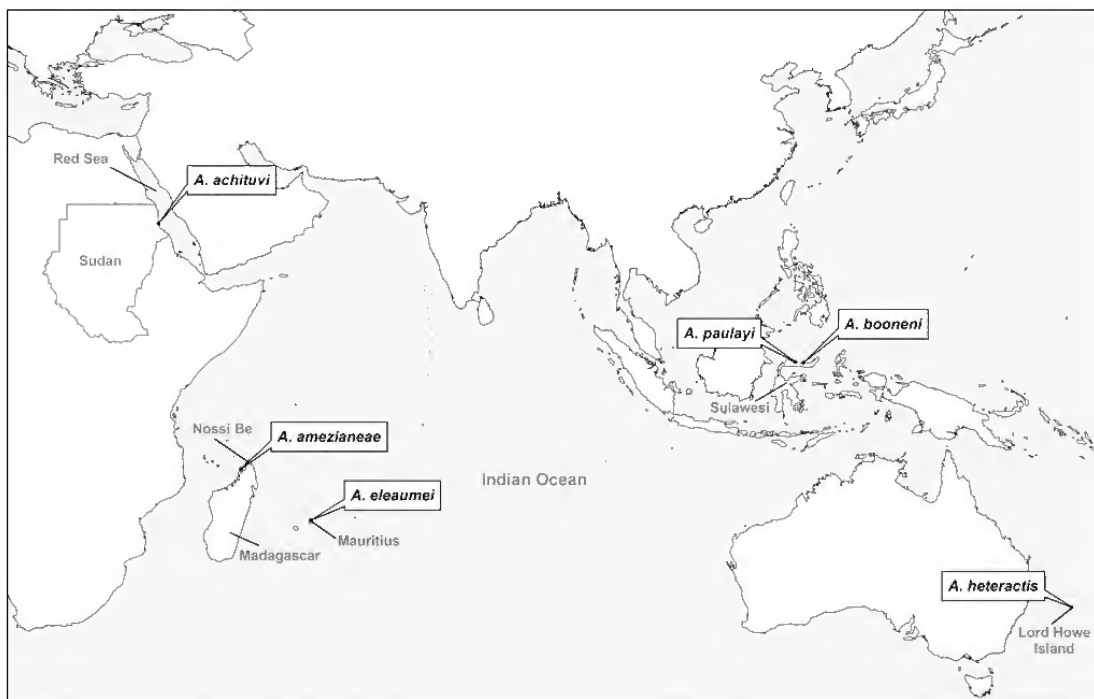


Figure 1. Distributions of the type localities of the six species of *Ailsastra* gen. nov.

madreporite, not fissiparous. Carinal series of plates narrowly visible, below adcarinal plates, doubly papulate, other ray plates slightly incurved proximally for 1 papula, 2 longitudinal series of papulae on each upper side of ray, 6 longitudinal series across mid-ray; disc close to regularly defined by 5 radial, 5 interradial plates; spinelets glassy, splay-pointed, subsacciform to conical, up to 14 spinelets in single or double series across proximal edge of plate, spinelets up to 0.15 mm long, 3–6 on distal interradial plates, proximal and distal spinelets subequal; some spinelets may act as pedicellariae, but not differentiated as valves; up to about 6 superomarginal spinelets per plate, up to about 14 inferomarginal spinelets per plate, longest distally, about twice length of superomarginal spinelets. Actinal spines per plate: oral 5; suboral 0–1; furrow (proximal) 3–4; subambulacral 3; adradial actinal 4–6; interradial 4–6; interradial spines glassy, conical, splay-pointed, in webbed tufts.

**Distribution.** Sudanese Red Sea.

**Etymology.** Named in recognition of the research on the asterinids of the eastern Mediterranean Sea and Red Sea by Dr Yair Achituv of the Bar Ilan University in Israel.

**Remarks.** The carinal plate arrangement and oral structure are consistent with this unique asterinid combination in the *Ailsastra* type species *A. paulayi*. The single specimen was not dissected. An absence of superambulacral and superactinal plates was not confirmed. Molecular data are not available for *A. achitui*.

#### *Ailsastra ameizianeae* sp. nov.

Figures 1, 2b, 3b, 4d–f

**Material examined.** Holotype (dry). NW Madagascar, Nossi Be, G. Cherbonnier, 6 Oct 1959, MNHN EcAs 11845.

Paratype (dry, part dissected). Type locality, G. Cherbonnier, 2 Dec 1959, MNHN EcAs 11846.

**Diagnosis.** *Ailsastra* with, at  $R = 10$  mm, discrete, short, broad rays,  $R/r$  about 1.5; 8 longitudinal series of papulae across mid-ray; abactinal spinelets stout, short, up to about 0.10 mm long; inferomarginal spinelets twice as long as superomarginal spinelets; up to 4 actinal interradial spines per plate.

**Description.** Integument evident; 5 rays,  $R$  up to 10 mm; rays discrete, short, wide at base, broad, tapered to narrow rounded end,  $R/r$  about 1.5; single madreporite, not fissiparous; abactinal gonopores. Carinal series of plates broadly visible, not below adcarinal plates, doubly papulate, other abactinal ray plates sometimes slightly incurved proximally for single papula, 3 longitudinal series of papulae on each upper side of rays, 8 longitudinal series of papulae at mid-ray; disc close to regularly defined by 5 radial, 5 interradial plates; spinelets glassy, stout, splay-pointed subsacciform, up to about 16 spinelets in double or single series across proximal edge of plates, up to about 0.10 mm long, up to 6 in subpaxilliform tuft on distal interradial plates, proximal and distal spinelets subequal; up to about 6 short stout sacciform superomarginal spinelets per plate, up to about 16 longer sacciform

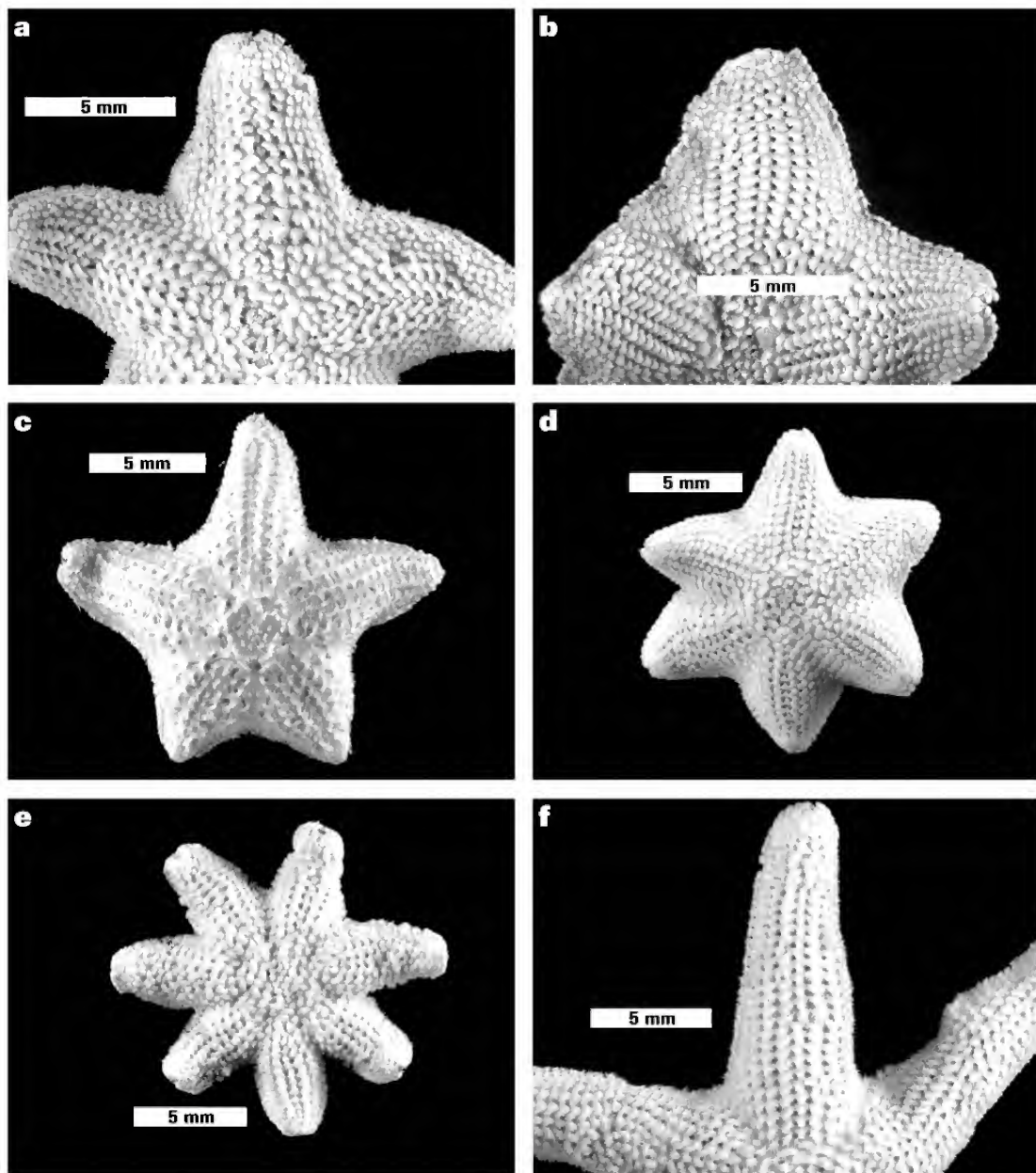


Figure 2. Abactinal view of holotypes of species of *Ailsastra* gen. nov. (photographed at same magnification). a, *Ailsastra achituvii* sp. nov., R = 10 mm, NHM 1951.5.7.12; b, *Ailsastra amezianae* sp. nov., R = 10 mm, MNHN EcAs 11845; c, *Ailsastra booneni* sp. nov., R = 9 mm, UF 1938; d, *Ailsastra eleaumei* sp. nov., R = 7.5 mm, MNHN EcAs 11843; e, *Ailsastra heteractis* (H.L. Clark, 1938), R = 7 mm, MCZ 3258; f, *Ailsastra paulayi* sp. nov., R = 16 mm, UF 1815.

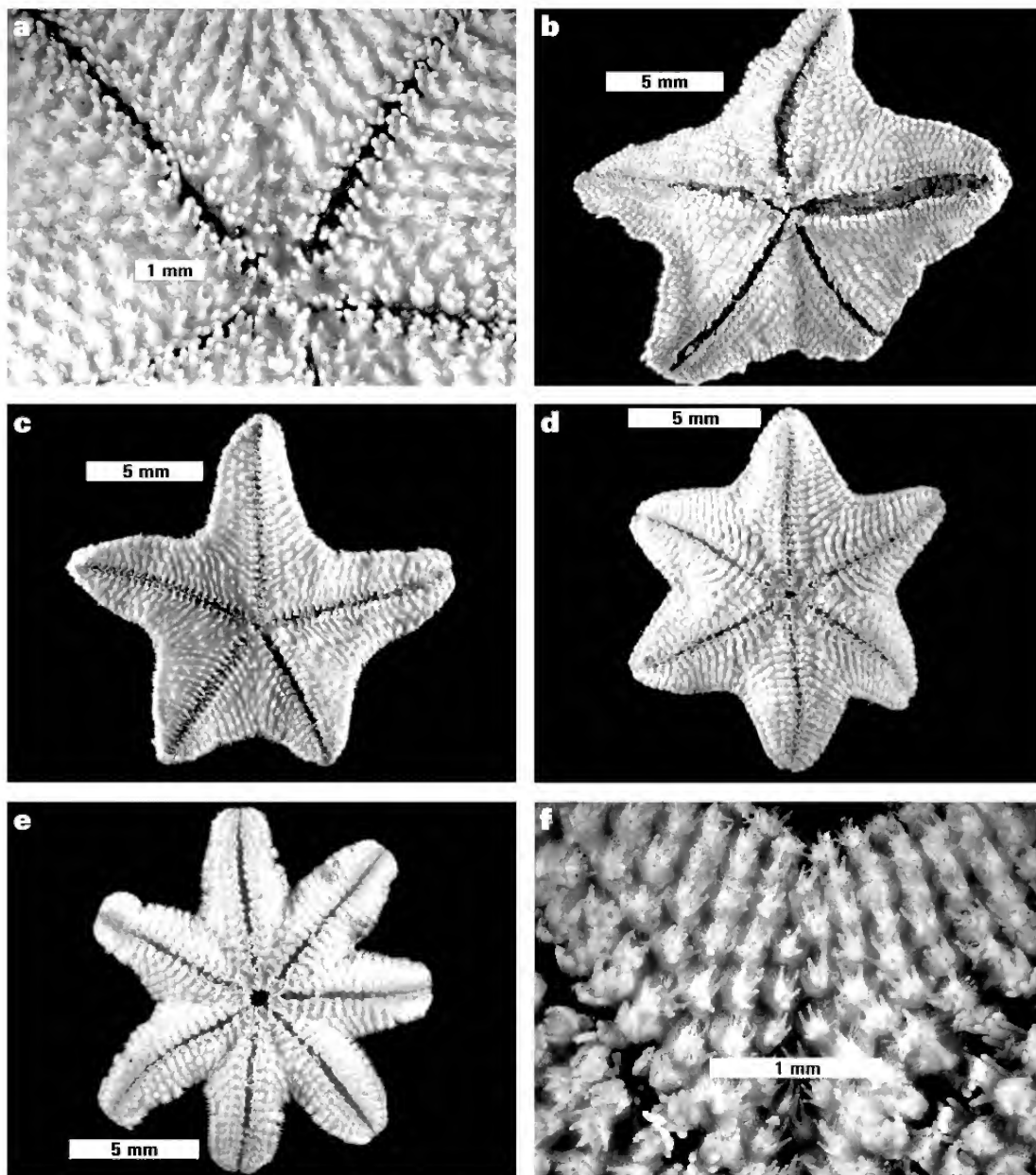


Figure 3. Actinal view of holotypes of species of *Ailsastra* gen. nov. a, *Ailsastra achituvu* sp. nov., R = 10 mm, NHM 1951.5.7.12; b, *Ailsastra amezianae* sp. nov., R = 10 mm, MNHN EcAs 11845; c, *Ailsastra booneni* sp. nov., R = 9 mm, UF 1938; d, *Ailsastra eleaumei* sp. nov., R = 7.5 mm, MNHN EcAs 11843; e, *Ailsastra heteractis* (H.L. Clark, 1938), R = 7 mm, MCZ 3258; f, *Ailsastra paulayi* sp. nov., R = 16 mm, UF 1815.



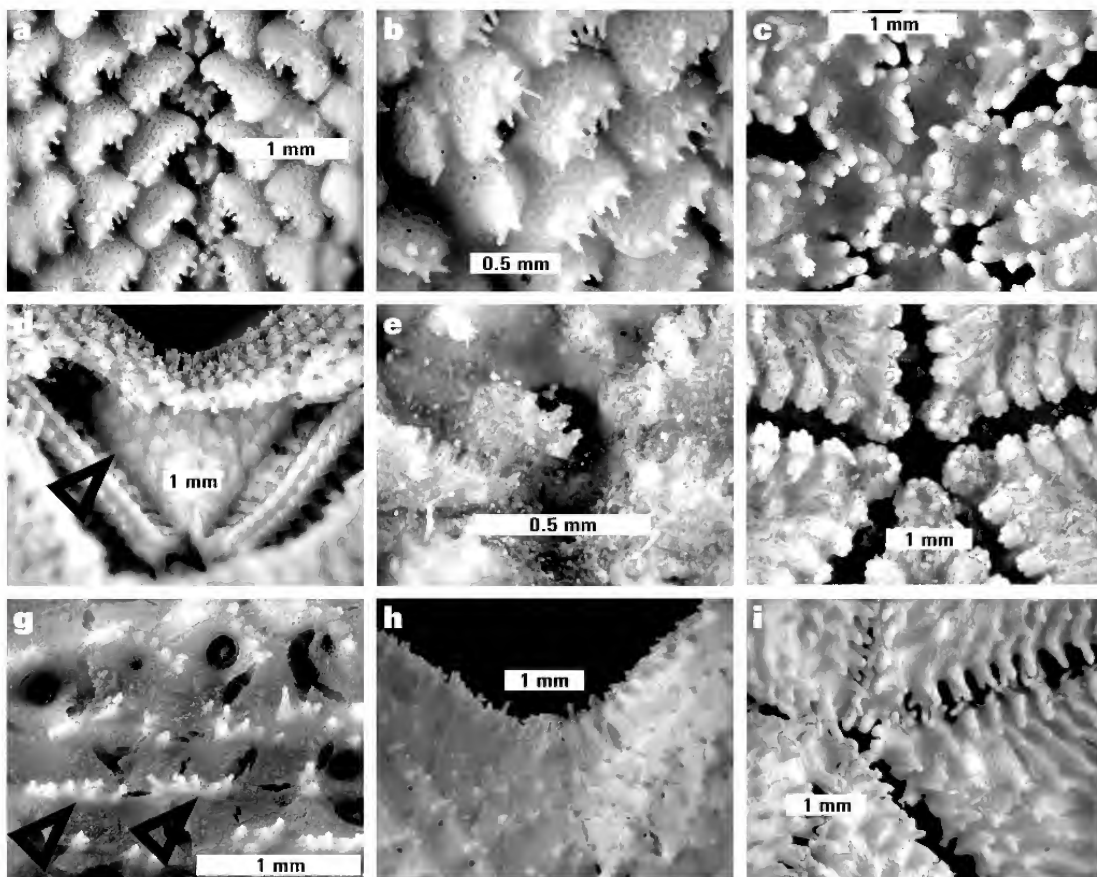


Figure 4. a–c, *Ailsastra achitavi* sp. nov., NHM 1951.5.7.12: a, low carinal series of plates; b, abactinal spinelets, glassy convexities on plates; c, small oral plates. d–f, *Ailsastra amezianeae* sp. nov.: d, abactinal interradial plates removed to show absence of superambulacral (arrow) and superactinal plates (paratype, MNHN EcAs 11846); e, abactinal spinelets (holotype, MNHN EcAs 11845); f, small oral plates (paratype, MNHN EcAs 11846). g–i, *Ailsastra boonenii* sp. nov., UF 1938: g, two proximal carinal plates with longitudinal series of spinelets (arrows), breaks in enveloping integument which obscures plates, abactinal spinelets; h, distal interradius, inferomarginal spinelets, absence of superomarginal spinelets; i, small oral plates, proximal interradial single pyramidal spines.

inferomarginal spinelets per plate, up to twice as long as superomarginal spinelets. Actinal spines per plate: oral 2–5; suboral 0; furrow (proximal) 3; subambulacral 2–3; adradial actinal 2–4; interradial 2–4; interradial spines stout, subsacciform, pointed, in webbed tufts.

**Distribution.** NW Madagascar, Nossi Be.

**Etymology.** Named in recognition of Dr Nadia Améziane of the Muséum National d'Histoire Naturelle, Paris, who has graciously assisted the authors with information and the loan of materials for echinoderm research.

**Remarks.** The carinal plate arrangement, oral structure, and absence of superambulacral and superactinal plates, are consistent with this unique asterinid combination in the *Ailsastra* type species *A. paulayi*. Molecular data are not available for *A. amezianeae*.

#### *Ailsastra boonenii* sp. nov.

Figures 1, 2c, 3c, 4g–i

**Material examined.** Holotype (alcohol). Indonesia, N Sulawesi I., Bay of Tomini, off Salongon, Mulibagu, 0°21'31"S, 124°3'14"E, 2–15 m, G. Paulay, 18 Sep 1999, UF 1938.

**Diagnosis.** *Ailsastra* with, at R = 9 mm, discrete, narrow rays, R/r up to 1.9; 6 longitudinal series of papulae across mid-ray; integument obscuring abactinal and actinal plates; abactinal spinelets granuliform to sacciform conical, up to about 0.20 mm long; lacking superomarginal spinelets; proximal actinal large pyramidal spines present on some interradia; up to 2 actinal interradial spines per plate.

**Description.** Integument obscures abactinal and actinal plates; 5 rays, asymmetrical form, R up to 9 mm; rays discrete, narrow, tapered to

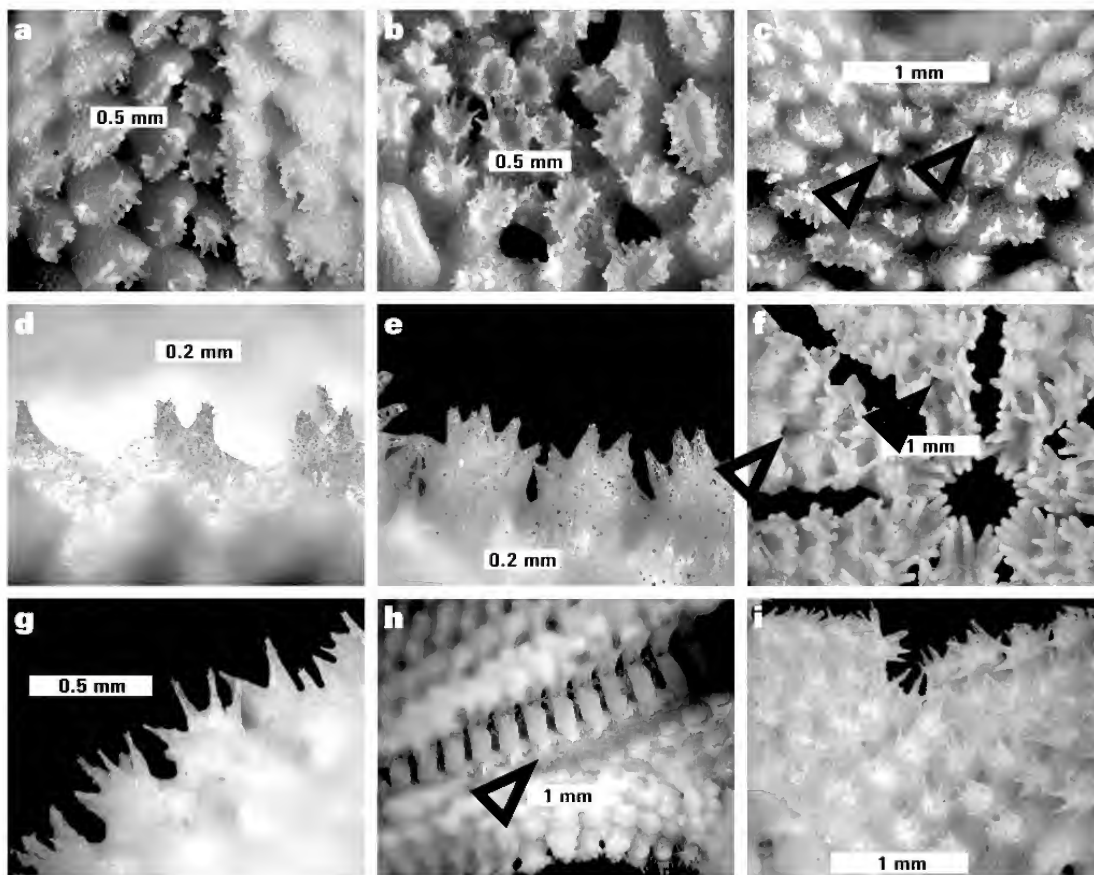


Figure 5. a–c, *Ailsastra eleaumei* sp. nov., MNHN EcAs 11843: a, low carinal series of plates with bowl-shaped spinelet arrangements; b, bowl-shaped arrangements of spinelets on disc plates; c, interradial abactinal gonopores (arrows). d–f, *Ailsastra heteractis* (H.L. Clark, 1938), MCZ 3258: d, lateral ray abactinal spinelets; e, inferomarginal spinelets; f, small oral plates, proximal actinal pores (arrows). g–i, *Ailsastra paulayi* sp. nov., UF 1815: g, abactinal spinelets; h, abactinal interradial plates removed to show absence of superambulacral plates (arrow); i, distal abactinal interradius.

narrow rounded end, R/r up to 1.9; single large madreporite, not fissiparous; abactinal paired or single interradial gonopores. Carinal series of plates extend to end of ray, below adcarinal plates creating furrow, each plate doubly papulate, other abactinal ray plates obscured by integument, crescentiform series of spinelets pointing through integument, single papula per plate, 2 longitudinal series of papulae on each upper side of rays, 6 longitudinal series of papulae across mid-ray; disc distinctly bordered by 5 radial, 5 interradial plates; spinelets glassy, stout, granuliform on upper ray, sacciform conical in interradius, up to about 0.20 mm long; up to 5 spinelets in longitudinal series on proximal carinal plates, 1–2 spinelets on carinal plates in mid ray, up to about 8 spinelets in predominantly single or double series across raised proximal edge of plates; single spinelets in mid-interradius; superomarginal plates lacking spinelets; up to about 8 long, thin, glassy spinelets per inferomarginal plate. Actinal plates obscured by integument, spines in oblique series, variably webbed by integument. Actinal

spines per plate: oral 3; suboral predominantly 1 (0–2), some longer than proximal oral spines, continuous as series with oral spines; furrow 3–2; subambulacral 2–1; adradial actinal 1; interradial 2–1; interradial spines digitiform, partly obscured by integument.

**Colour (live).** Mottled dark mauve and white, disc reddish-brown (holotype photo by G. Paulay: GP Sula-664).

**Distribution.** Indonesia, N Sulawesi, 2–15 m.

**Etymology.** Named in appreciation of the assistance of Ben Boonen, who has graciously and skilfully prepared the images for this and other echinoderm papers.

**Remarks.** The carinal plate arrangement and oral structure are consistent with the patterns shown in the type species, *Ailsastra paulayi*. The holotype was not dissected and the absence of

superambulacral and superactinal plates was not confirmed. Molecular phylogenetic analysis by Jon Waters (pers. comm.; paper in preparation) places this species in a clade with the type species, *Ailsastra paulayi* (below).

***Ailsastra eleaumei* sp. nov.**

Figures 1, 2d, 3d, 5a–c

*Material examined.* Holotype (dry). Mauritius (Île Maurice), MAU 74-12, Peyrot-Clausade, 1974, MNHN EcAs 11843.

Paratype (dry, part dissected). Type locality, MAU 74-13, MNHN EcAs 11844.

*Diagnosis.* *Ailsastra* with, at  $R = 7.5$  mm, discrete, short, strongly tapered rays,  $R/r$  about 1.6; frequent bowl-shaped arrangement of numerous, small, thin, webbed spinelets on abactinal plates, up to 0.17 mm long; 4 longitudinal series of papulae across mid-ray; up to 5 interradial actinal spines per plate; longitudinal alignment of spines on some distal actinal plates.

*Description.* Integument not evident; rays 6 (holotype), 5 (paratype),  $R$  up to 7.5 mm; rays discrete, short, strongly tapered, rounded distally,  $R/r$  about 1.6; single madreporite, not fissiparous; abactinal gonopores. Carinal series of plates variably narrowly evident below adcarinal plates, doubly papulate, other abactinal ray plates lacking papular indentation, single longitudinal series of non-carinal papulae on each upper side of rays, 4 longitudinal series of papulae across mid-ray; disc not delineated; spinelets glassy, thin, subsacciform to conical, finely splay-pointed, up to about 20 spinelets in 2 webbed series across proximal edge of plate, frequently in bowl-shaped series around periphery of projecting plate, up to about 0.17 mm long, up to 8 in subpaxilliform tuft on distal interradial plates; proximal and distal spinelets subequal; up to about 10 webbed spinelets around periphery of each superomarginal plate, up to about 16 longer spinelets on each inferomarginal plate, most in peripheral webbed series on abactinal surface of plate, few on actinal surface. Some non-plated areas actinally. Actinal spines per plate: oral 4; suboral 0; furrow 3; subambulacral 3; adradial actinal 1–3; interradial 1–3, up to 5 distally, sometimes in longitudinal alignment; interradial spines sacciform, thin, pointed.

*Distribution.* Mauritius (Île Maurice).

*Etymology.* Named in recognition of Marc Eleaume of the Muséum National d'Histoire Naturelle, Paris, who has graciously assisted the authors with information and the loan of materials for echinoderm research.

*Remarks.* The carinal plate arrangement, oral structure, and absence of superambulacral and superactinal plates are consistent with the type species. Variable ray number is common amongst asterinid species, and the predominant ray number for *A. eleaumei* is not evident. Molecular data are not available for *A. eleaumei*.

***Ailsastra heteractis* (H.L. Clark)**

Figures 1, 2e, 3e, 5d–f

*Asterina heteractis* H.L. Clark, 1938: 152–153, pl. 22 fig. 5.—H.L. Clark, 1946: 130, 133.—Rowe (in Rowe and Gates), 1995: 34–35.

*Aquilonastra heteractis*.—O'Loughlin and Waters, 2004: 11, 13, 15.

*Material examined.* Holotype (dry). Australia, Lord Howe I., Neds Beach, under rock fragment, littoral, K. Birmingham, Apr 1932, MCZ 3258.

Paratypes (dry). Lord Howe, Neds Beach, MCZ 3259 (1); dredged from lagoon near Goat I., MCZ 3260 (2).

Other material (dry). Queensland, Townsville, AM J9541 (2); reef flat, Heron I., AM J19449 (1).

*Diagnosis.* *Ailsastra* with 6–7 discrete high rays with narrow bases,  $R/r$  about 2.0; multiple inconspicuous madreporites; fissiparous habit; abactinal gonopores; spinelets up to 0.15 mm long; large proximal actinal interradial pores; up to 4 spines per actinal interradial plate.

*Description.* 6–7 rays,  $R$  up to 7 mm; integument evident; rays discrete, narrow base, long, blunt distally, high convex abactinally,  $R/r$  about 2.0; multiple inconspicuous madreporites; fissiparous, ray lengths frequently unequal; abactinal paired interradial proximal gonopores. Carinal series of plates broadly visible, slightly below adcarinal plates, doubly papulate for most of ray, not proximally, other ray plates slightly indented for single large papula, single longitudinal series of papulae on each upper side of rays, 4 longitudinal series across mid-ray; papular spaces large; disc not delineated; spinelets glassy, stout, conical to subsacciform, splay-pointed, up to about 8 per plate, in single or double series across plates or in apical tufts, up to 0.15 mm long; superomarginal plates with up to 4 spinelets; inferomarginal plates with up to 10 longer, splay-pointed webbed spinelets. Single large proximal actinal interradial pores. Actinal spines per plate: oral 4–6; suboral 0–3; furrow (proximal) 3–4; subambulacral 3–4; adradial actinal 2–4; interradial 1–3; interradial spines subsacciform, elongate, pointed.

*Colour (live).* Salmon pink to light orange to nearly white abactinally, whitish actinally (H.L. Clark, 1938).

*Distribution.* Lord Howe I., NE Australia, littoral to shallow sublittoral.

*Remarks.* The presence of large single proximal actinal pores is unique amongst the asterinids. There was inadequate material to confirm by dissection the nature of the pores. They were observed only on the holotype. The distal oral spines are close to the suboral spines on the characteristic small oral plates, and sometimes appear to be in continuous series. O'Loughlin and Waters (2004) assigned *Asterina heteractis* to *Aquilonastra* O'Loughlin, 2004, but noted some exceptional characters. *A. heteractis* has the carinal plate arrangement and small oral plates of *Ailsastra paulayi*, the type species of *Ailsastra*, and is reassigned to this new genus. No specimen was dissected to confirm an absence of superambulacral and superactinal plates.

***Ailsastra paulayi* sp. nov.**

Figures 1, 2f, 3f, 5g–i

*Material examined.* Holotype (in alcohol, part dissected). Indonesia, Sulawesi I., Pulau Talatakoh, 0°28'2"S, 122°8'22"E, 1–10 m, G. Paulay, 19 Sep 1999, UF 1815.

Paratype. Sulawesi I., 1–2°S, 121°E, 1–16 m, G. Paulay, 26 Sep 1999, UF 910.

*Diagnosis.* *Ailsastra* with, at  $R = 16$  mm, discrete, elongate, narrow, slightly tapered rays,  $R/r$  about 2.7; 8 longitudinal series of papulae across mid-ray; disc regularly bordered; long, thin, spinelets, up to about 0.25 mm long; proximal and distal interradial spinelets subequal; superomarginal and inferomarginal spinelets subequal; up to 7 actinal interradial spines per plate.

**Description (holotype).** Morphological characters of *Ailsastra*; integument evident; 5 rays, R up to 16 mm; rays discrete, narrow at base, elongate, low, slightly tapered, rounded distally, R/r about 2.7; single madreporite, not fissiparous; abactinal gonopores. Carinal series of plates broadly visible, plates not noticeably below adcarinal plates, doubly papulate, other ray plates not indented for single papula, 3 longitudinal series of papulae on each upper side of rays, 8 longitudinal series across mid-ray; disc regular, defined by 5 radial, 5 interradial plates; spinelets glassy, thin, subsacciform to conical, each with few small points distally, up to about 20 spinelets in single or double webbed series across proximal edge of plate, or in splayed tufts on plates, spinelets up to about 0.25 mm long on proximal ray, up to about 10 in subpaxilliform splayed tuft on distal interradial plates; proximal and distal interradial spinelets subequal in length; superomarginal and inferomarginal spinelets subequal in length, up to about 6 per superomarginal plate, about 14 per inferomarginal plate. Actinal spines per plate: oral 5–6; suboral 0–1; furrow (proximal) 5; subambulacral 4; adradial actinal 3; interradial 3–7; interradial spines glassy, thin, subsacciform to conical, splay-pointed, in webbed tufts.

**Colour (live).** Mottled red and orange (holotype photo by G. Paulay: GP 670:24).

**Distribution.** Indonesia, Sulawesi; 1–16 m.

**Etymology.** Named in recognition of Dr Gustav Paulay of the University of Florida, who collected this material and who has facilitated extensive collecting of asterinid material throughout the Indo-Pacific region.

**Remarks.** The paratype is small (R = 7 mm), and the rays are not as narrow as those of the holotype. Molecular phylogenetic data from Jon Waters (pers. comm.) places the two specimens of *A. paulayi* in a highly divergent but strongly monophyletic clade within a molecular phylogeny of Asterinidae (Jon Waters, pers. comm.; paper in preparation).

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## A review of soles of the genus *Aseraggodes* from the South Pacific, with descriptions of seven new species and a diagnosis of *Synclidopus*.

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### Abstract

Randall, J.E. 2005. A review of soles of the genus *Aseraggodes* from the South Pacific, with descriptions of seven new species and a diagnosis of *Synclidopus*. *Memoirs of Museum Victoria* 62(2): 191–212

The soleid genus *Parachirus* Matsubara and Ochiai is referred to the synonymy of *Aseraggodes* Kaup. *Aseraggodes persimilis* (Günther) and *A. ocellatus* Weed are reclassified in the genus *Pardachirus* Günther. *Synclidopus macleayanus* (Ramsay) from Queensland and NSW is redescribed. A diagnosis is given for *Aseraggodes*, and a key and species accounts provided for the following 12 species of the genus from islands of Oceania in the South Pacific and the east coast of Australia: *A. auroculus*, sp. nov. from the Society Islands; *A. bahamondei* from Easter Island and Lord Howe Island; *A. cyclurus*, sp. nov. from the Society Islands; *A. lateralis*, sp. nov. from the Marquesas Islands; *A. lenisquamis*, sp. nov. from NSW; *A. magnoculus* sp. nov. from New Caledonia; *A. melanostictus* (Peters) from 73 m off Bougainville and a first record for the Great Barrier Reef from 115 m; *A. nigrocirratus*, sp. nov. from NSW; *A. normani* Chabanaud from southern Queensland and NSW; *A. pelvicus*, sp. nov. from the Great Barrier Reef; *A. ramsaii* (Ogilby) from Lord Howe Island, with a first record for New Caledonia; and *A. whitakeri* Woods as first records from the Caroline Islands, Coral Sea, New Caledonia, Fiji, American Samoa, Phoenix Islands, and Society Islands. Presumed hybrids of *A. lenisquamis* and *A. nigrocirratus* were found in two Australian Museum lots of specimens from NSW.

### Keywords

Taxonomy, soleid fishes, *Aseraggodes*, *Synclidopus macleayanus*

### Introduction

With the advent of scuba diving and the use of the ichthyocide rotenone, ichthyologists have made major collections of shore fishes, particularly in the tropical and subtropical regions of the world. The coral reefs and adjacent habitats have yielded a multitude of new species of fishes. Taxonomic research tended to focus on the colourful species in well-known genera with ample material. Collections rarely resulted in more than one or two specimens of soles of any species of *Aseraggodes* Kaup. Small and usually not distinctly coloured, they have not received the scientific attention they require. As noted by Randall (1996), some specimens of *Aseraggodes* still remain on museum shelves identified only to genus or the family Soleidae.

Nevertheless, the genus *Aseraggodes* is second only to *Solea* in the number of species of the family Soleidae. Eschmeyer's *Catalog of Fishes* (updated to 14 January 2005 at web site [www.calacademy.org/research/ichthyology/catalog/fishcatsearch.html](http://www.calacademy.org/research/ichthyology/catalog/fishcatsearch.html)) lists 26 Indo-Pacific species as valid for the genus and one, *A. herrei* Seale, from the Galápagos Islands. Of the 26 species of Eschmeyer's list, *A. filiger* Weber, with its slender body and filamentous first dorsal ray, should remain in the monotypic genus *Coryphillus* Chabanaud, 1932. *Aseraggodes persimilis* (Günther) from New Britain and

*A. ocellatus* Weed from Sri Lanka, both described as having a pore at the base of most of the dorsal and anal rays, are here reclassified as synonyms of *Pardachirus pavoninus* (Lacepède). The species of *Aseraggodes* lack these distinctive externally visible pores.

Clark and George (1979) showed that basal dorsal- and anal-ray pores in species of *Pardachirus* are the release sites for a powerful toxin when these soles are threatened. Randall and Meléndez (1987) reported what seems to be a comparable skin toxin in *Aseraggodes bahamondei* at Easter Island. They found small pores beneath occasional scales toward the periphery of the body on the ocular side, which they believe elicit the toxin. Randall (2002) discovered that *A. therese* in the Hawaiian Islands is unpalatable to the jack *Caranx melampygus*. He did not examine specimens of *therese* for pores at that time, but after long searching and with the help of staining, these were later detected beneath a few scales on a large non-type specimen. Finding the pores on small specimens or old museum specimens is difficult. These pores were detected in this study only in *A. melanostictus* and one of the new species, but they are probably present in some other species as well.

*Solea macleayana* was described by Ramsay (1881) from NSW. Ogilby (1916) illustrated the species, described it more



fully, and reclassified it in *Aseraggodes*. He has been followed by subsequent authors. Chabanaud (1943), however, selected *Solea macleayana* as the type species of a new genus, *Synclidopus*, one of eight new soleid genera briefly described in the paper. The type species of *Synclidopus* is more fully described here.

The classification of the species *Aseraggodes* has been difficult because of the paucity of specimens, ontogenetic changes, variability in colour pattern (see Figs 3–5), and the broad range in the counts of dorsal rays, anal rays, and lateral-line scales. For example, Randall and Meléndez (1987) found a range of seven dorsal rays, eight anal rays, and 12 lateral-line scales for 27 specimens of *A. bahamondei*, and Randall, 2002 reported 29 specimens of *A. therese* with a range of eight dorsal rays, eight anal rays, and seven lateral-line scales. Nevertheless, the combination of these three counts will often be of diagnostic value to the species of the genus. The number of vertebrae also may vary within a species, though usually not more than two or three. Ochiai (1963) reported 34–37 vertebrae for 67 specimens of the Japanese species *A. kobensis* (Steindachner).

The species of *Aseraggodes* generally have a thin membranous ridge along the dorsal and anal rays, often disappearing on posterior rays, and many species have cirri along the edges of these ridges, especially on anterior rays. In old museum specimens or poorly preserved specimens, the ridges may not be apparent, and the cirri often cannot be detected. This limits the usefulness of these features as diagnostic characters.

Twelve species of *Aseraggodes* have been reported from eastern Australia and the islands of the Oceania. Peters (1877) described *A. melanostictus* from a specimen collected in 73 m off Bougainville. Ogilby (1889) named *A. ramsaii* from one specimen from Lord Howe Island. Norman (1926) reported three specimens, 130–142 mm total length, from Queensland as *A. melanostictus*. Chabanaud (1930a) realized that these were not correctly identified and described a 135-mm one as a new species, *A. normani*. Schultz (1943) reported a small specimen of the genus from Hull Island in the Phoenix Islands. He wrote, "It may be a specimen of *Aseraggodes melanostictus* (Peters)." Woods in Schultz and collaborators (1966) described *A. whitakeri* and *A. smithi* as new species from the Marshall Islands. He identified a specimen from Kwajalein Atoll, Marshall Islands as *Aseraggodes melanostictus* "with uncertainty." Randall and Meléndez (1987) named *A. bahamondei* from Easter Island and Lord Howe Island. Randall (1996) described *A. borehami* and *A. therese*, and Randall (2002) added *A. holcomi*, all three from the Hawaiian Islands. Randall and Bartsch (2005) determined that the Marshall Islands specimen identified as *A. melanostictus* by Woods is a new species, *A. heraldi*, described *A. firmisquamis* from Palau, and reported *A. smithi* from Palau. The present paper provides the descriptions of seven new species of *Aseraggodes* from the South Pacific, as well as range extensions for *A. melanostictus*, *A. ramsaii*, and *A. whitakeri*.

**Materials and methods.** Type specimens of *Aseraggodes* have been variously deposited at the Australian Museum, Sydney (AMS); Natural History Museum, London (BMNH); Bishop Museum, Honolulu

(BPBM); California Academy of Sciences, San Francisco (CAS); Museum Victoria, Melbourne (NMV); National Science Museum, Tokyo (NSMT); Royal Ontario Museum, Toronto (ROM); and US National Museum of Natural History, Washington, DC (USNM).

Standard length (SL) is measured horizontally from the front of the upper lip to the base of the caudal fin (end of hypural plate). Body depth is the maximum distance between the bases of the dorsal and anal fins. Body width is the maximum thickness midlaterally between the ocular and blind surfaces. Head length (HL) is measured from the front of the upper lip to a vertical at the posterior end of the operculum. Preorbital length is the distance from the front edge of the upper eye directly forward to the most anterior edge of the head. Snout length is taken from the front of the upper lip to the nearest edge of the upper eye. Eye diameter is the greatest diameter of the lower eye (the dark eyeball, not the surrounding cutaneous part). The interorbital width is the vertical distance between horizontal lines at the lower edge of the upper eye and upper edge of the lower eye (i.e. between the dark edges of the two eyes). Upper jaw length is measured on the blind side from the front of the upper lip to the rear edge of the maxilla (often too difficult to determine the posterior end of the maxilla on the ocular side). Caudal-peduncle depth is the least depth, or if the caudal peduncle is absent, the depth is measured at the base of the caudal fin. Caudal-peduncle length is the horizontal distance between verticals at the rear base of the anal fin and the base of the caudal fin at its ventral edge. Lengths of fin rays are measured from the ray base in a straight line to the tip. Caudal-fin and pelvic-fin measurements are the length of the longest ray.

Tables 1–3 provide the counts of the dorsal rays, anal rays, and lateral-line scales, respectively. Proportional measurements of the new species are given in Tables 4–11 as percentages of the standard length. Measurements (ratios related to SL, head length, or body depth) in the text are rounded to the nearest 0.05. Data in parentheses in the descriptions refer to paratypes.

Lateral-line scales are counted from the base of the caudal fin to the front of the straight part of the lateral line on the head (hence 5–15 scales anterior to the upper end of the gill opening). Scale counts above and below the lateral line are the maximum number of scales in an oblique row between the lateral line and the outer edge of the scaly sheath at the base of the dorsal and anal fins, respectively.

Vertebral counts for soles are often given in two parts, the abdominal vertebrae, followed by the caudal vertebrae. There are ten abdominal vertebrae in all the species of *Aseraggodes* examined (the count includes the very small first vertebra overlooked by some authors), so only the total count, which includes the urostyle, is given here, which includes the urostyle.

Ochiai (1963) used the count of the number of dorsal pterygiophores (he called these interneural spines) associated with the first three vertebrae (actually, four as he did not include the first very small vertebra) as a taxonomic character. He is followed in the use of this count.

### *Synclidopus* Chabanaud, 1943

*Synclidopus* Chabanaud, 1943: 291.

**Type species.** *Solea macleayana* Ramsay, 1881.

**Diagnosis.** Dorsal rays 62–66; anal rays 49–53; caudal rays 18–20; pelvic rays 5, the fifth ray of ocular-side fin joined by membrane to base of first anal ray; lateral-line scales 96–113; lateral line extending forward on head to within an eye diameter of upper eye; a second lateral line branching off dorsally on head, about two eye diameters behind upper eye, angling sharply posteriorly about 8 scale rows beneath naked part of

dorsal fin, and continuing onto anterior body; body deep, the depth 2.2–2.25 in SL; head short and obtuse, its length 5.25–5.5 in SL; eyes small, 8.1–9.0 in HL; tubular anterior nostril short, not reaching lower eye when laid back; rays of median fins short; anus and genital papilla on blind side, adjacent to base of first anal ray; no pore at base of dorsal and anal rays, and no small pores detected beneath scales of ocular side; vertebrae 36–38; dorsal pterygiophores anterior to fourth neural spine 7; unique colour pattern of many narrow dark bars on ocular side of head and body.

**Remarks.** The type species of this monotypic genus was first described in *Solea* Cuvier. Other authors such as Ogilby (1916), Norman (1926), McCulloch (1929), Allen et al. (1976), and Grant (1987) classified it in *Aseraggodes* Kaup. It is clearly distinct at the generic level from *Aseraggodes* by having a second lateral line on the ocular side of the head that continues dorsoanteriorly on the body, the deepest body, shortest and most obtuse head, smallest eyes, anus and genital papilla on the blind side, highest number of lateral-line scales (96–113, compared to 53–96 for species of *Aseraggodes*), 7 dorsal pterygiophores anterior to fourth neural spine (species of *Aseraggodes* with 7–16; only one with 7 or 8), and the colour pattern of narrow dark bars. Ogilby (1916) reported the maximum size as 280 mm total length (largest species of *Aseraggodes*, 192 mm TL).

#### *Synclidopus macleayanus* (Ramsay, 1881)

##### Figure 1

*Solea Macleayana* Ramsay, 1881: 462.

*Solea fluviatilis* Ramsay, 1882: 111 (type locality, Hunter River, NSW).

**Material examined.** NSW: Port Jackson, AMS I.16278-01, 135 mm, syntype of *Solea macleayana*, Eight miles from North Head, Richmond River, R/V “Endeavour”, BMNH 1925.7.22.72, 112 mm. Sydney, Hawkesbury River, Gentleman’s Halt, AMS I.19951-003, 6: 72–105 mm. Off Sydney, 33°51’S, 151°18’E, 40–45 m, BPBM 39454, 149 mm. Lord Howe Island: AMS I.12664, 103 mm.

**Type locality.** Manly Beach, Port Jackson, NSW.

**Remarks.** Ramsay (1881) briefly described this species. He wrote, “A number were taken in the net at Manly Beach, September 11th, 1880, with *Solea microcephala*.” Only one type specimen of *Solea macleayana* has been found, labeled as a syntype at the Australian Museum. A more detailed description of the species was provided by Ogilby (1916: 127, pl. 15) who had three specimens, 154–192 mm in total length. He described the colour as “Lavender grey, with from 32–36 narrow brown cross-bars, which are usually rather wider than the interspaces, and of which 6 or 7 are on the head and 1 or 2 on the base of the caudal fin; ...” He placed *Solea fluviatilis* Ramsay, described from one 76-mm specimen from freshwater in Hunter River, in synonymy, adding that Ramsay was “possibly misled by the different character of the element in which it was found.” Ogilby summarized the reproductive cycle. Adults spend the winter months in moderately deep water, gradually move to shallower water in spring. On reaching



Figure 1. *Synclidopus macleayanus*, BPBM 39454, 149 mm SL, off Sydney, NSW.

maturity during summer months, they collect in the vicinity of river mouths, where they spawn. “The young fishes, as soon as the yolk-sac is absorbed, make their way into the estuaries and gradually work up these even to far beyond the limit of the tide, as we know from the Hunter River example ...” Under the heading *Uses*, Ogilby wrote, “A delicious pan-fish, fully equal in flavor to its famous European relative, *Solea solea*.”

Norman (1926) gave the distribution of this species as “Coasts of New South Wales and southern Queensland (from southern NSW to Caloundra).” Allen et al. (1976: 437) reported a specimen from Lord Howe Island.

Grant (1987) noted that this sole is adept at burrowing beneath the sand and “actually swims beneath the sand.” He summarized the food habits as “shellfish and worms that live on and in the substrate.”

#### *Aseraggodes* Kaup, 1858

*Aseraggodes* Kaup, 1858: 103.

*Parachirus* Matsubara and Ochiai 1963: 93 (type species, *Parachirus xenichus* Matsubara and Ochiai, 1963 opening by original designation and monotypy).

**Type species.** *Aseraggodes guttulatus* Kaup, 1858, by subsequent designation of Jordan and Evermann, 1898.

**Diagnosis.** Dorsal rays 58–79; anal rays 39–61; caudal rays typically 18 (usually 14–16 branched in adults); no pectoral fins; pelvic rays normally 5; lateral-line scales 39–96 (including those extending onto head); no gill rakers; abdominal vertebrae 10 (including the first vertebra, not counted by some authors, very narrow, the neural spine slender and short, not extending above cranium); total vertebrae 33–40; first two dorsal pterygiophores joined to a thicker bone (termed the erisma and counted as the first pterygiophore, though branched distally to support the first two dorsal rays), its origin between second neural spine and cranium, 7–16 dorsal pterygiophores anterior to fourth neural spine; body an elongate oval, the depth 2.0–2.8 in SL, and very thin; eyes on right side, elevated, separated by a narrow scaled space; upper eye in advance of lower eye (rarely directly above); caudal peduncle, if present, very short; scales small, ctenoid (except cycloid lateral-line scales); a straight lateral line midlaterally on both sides, with a short anterodorsal branch on blind side; no prominent pore at base of dorsal and anal rays; gill membranes united, free from isthmus,

the lower part of head scaled over from ocular to blind side; mouth ventral and small; jaws strongly curved; a band of villiform teeth on blind side of jaws; two nostrils on each side, the anterior nostril of ocular side tubular, but not longer than eye diameter; posterior nostril of ocular side a narrow opening in labial groove before lower eye; dorsal fin originating anteriorly on snout, the first ray not prolonged; caudal fin rounded to slightly pointed, not broadly connected by membrane to dorsal and anal fins; pelvic fins on ventral edge of body, close together anteriorly, adjacent or with ocular-side fin slightly anterior; anus anterior or ventroanterior to first anal ray. Sciatic part of urohyal forming an angle of about 60–85° to horizontal main part of bone.

**Remarks.** Kaup (1858: 103) briefly described *Aseraggodes guttulatus* as a new genus and species, but gave no locality for the holotype, as noted by Günther (1862: 477). Chabanaud (1930b) revised the 15 species of the genus then known. He mistakenly placed *A. kaianus* (Günther) in the synonymy of *A. guttulatus* and gave two localities, Kei Islands (Günther's type locality of *kaianus*) and the Maldives Islands. Desoutter et al. (2001) resolved the locality problem by finding the holotype in the Muséum National d'Histoire Naturelle (MNHN 1246, 79.0 mm SL). Kaup's original label indicated the specimen as the type and the collection locality as Bourbon (= Réunion).

Kaup wrote in his description of *Aseraggodes guttulatus* that the height of the body is half the total length. Günther (1862: 477) questioned this in a footnote. Martine Desoutter (pers. comm.) measured the height of the body of the holotype as 3.1 in total length. She confirmed Kaup's counts of the dorsal and anal rays as 64 and 42, respectively. She also provided the lateral-line scale count of 84 and an x-ray, which indicates a vertebral count of 34, and 14 dorsal pterygiophores before the fourth neural spine.

Matsubara and Ochiai (1963) described *Parachirus xenicus* as a new genus and species of sole from Japan. In a review of the Soleidae and Cynoglossidae of Japanese waters, Ochiai (1963) separated *Parachirus* from *Aseraggodes* by having the dorsal, anal, and pelvic fins slightly branched (as opposed to not branched in *Aseraggodes*), the tubular anterior nostril reaching the edge of the lower eye (not reaching in *Aseraggodes*), vertebrae 32–33, revised in this paper to 33–34 because the tiny first vertebra is now included in the vertebral count (vs 37–39 vertebrae in *Aseraggodes*), about 15 inter-neural spines (= dorsal pterygiophores) associated with the anterior 4 neural spines, and the pelvic fins attached by membrane to the genital papilla. In a generally favorable review of Ochiai's publication, Hubbs (1967) pointed out its limitation from dealing mainly with Japanese species. Chapleau (1989) made a study of the anterior dorsal pterygiophores, erisma, and neural spines of 41 species of 26 genera of soleid fishes. He recognized *Parachirus* as a valid genus; however, he included only four species of *Aseraggodes* in his study.

This study of *Aseraggodes* has shown that the dorsal, anal and pelvic fins may be simple or branched (the young of those with branched rays have unbranched rays); the tubular anterior nostril often reaches the edge of the lower eye; the vertebrae vary from 33 to 40; the dorsal pterygiophores anterior to the fourth neural spine vary from 7 to 15; and the

pelvic fins may be attached by membrane to the genital papilla (as in *A. normani*). Therefore, *Parachirus* is a synonym of *Aseraggodes*.

### Key to species of *Aseraggodes* of the South Pacific

1. Caudal peduncle present, though very short (7.2–10.8 in HL) ..... 2
- No caudal peduncle (rear base of anal fin below or posterior to base of lowermost caudal ray) ..... 5
2. Dorsal and anal rays short, the longest dorsal ray 1.9–2.15 in HL; dorsal and anal rays unbranched (young to adults); vertebrae 39–40; dorsal pterygiophores (including erisma) anterior to fourth neural spine 7–8; maximum size 156 mm SL (Easter Island and Lord Howe Island) *A. bahamondei*
- Dorsal and anal rays not short, the longest dorsal ray 1.25–1.8 in HL; dorsal and anal rays of adults branched; vertebrae 36–38; dorsal pterygiophores anterior to fourth neural spine 13–15; largest specimen, 67.5 mm ..... 3
3. Head large, its length 4.1–4.35 in SL; body slender, the depth 2.55–2.75 in SL; largest specimen, 43 mm SL (Micronesia and New Caledonia to Society Islands) .... *A. whitakeri*
- Head not large, its length 4.45–4.75 in SL; body not slender, the depth 2.4–2.6 in SL; attains at least 63 mm SL ..... 4
4. Longest dorsal ray 1.25 in HL; length of caudal fin 3.4 in SL; HL 4.75 in SL; pelvic fins long, 1.6 in HL; lateral-line scales 81; edge of membranous ridge of anterior dorsal rays with a row of small tubercle-like papillae, many ending in a tiny cirrus (one specimen, 67.5 mm SL, Swain Reefs, Great Barrier Reef) ..... *A. pelvicus*
- Longest dorsal ray 1.65–1.7 in HL; length of caudal fin 3.85–3.95 in SL; HL 4.45–4.5 in SL; pelvic fins not long, 2.3–2.35 in HL; lateral-line scales 86–88; edge of membranous ridge of anterior dorsal rays without a row of papillae or cirri (Lord Howe Island and New Caledonia) ..... *A. ramsaii*
5. Lateral line of ocular side with 3 branches on head; membrane from last rays of pelvic fins joined to genital papilla (NSW and southern Queensland) ..... *A. normani*
- Lateral line of ocular side without branches on head; no membrane linking last ray of pelvic fins to genital papilla ..... 6
6. Dorsal, anal, and pelvic rays unbranched; lateral-line scales 78–79 (2 specimens, 74–86.5 mm SL, Bougainville and Great Barrier Reef, 73–115 m) .... *A. melanostictus*
- Dorsal, anal, and pelvic rays of adults branched; lateral-line scales 61–73 ..... 7
7. Lateral-line scales 61–68; dorsal rays 62–70; anal rays 46–52; dorsal pterygiophores anterior to fourth neural spine 8–9 ..... 8
- Lateral-line scales 69–73; dorsal rays 67–77; anal rays 49–57; dorsal pterygiophores before fourth neural spine 10–12 ..... 9
8. Surface of scales smooth, the posterior edge somewhat pointed, with only the tips of ctenii visible; snout length 2.45–2.5 in HL; caudal-peduncle depth 1.25–1.45 in HL;

- caudal-fin length 4.6–5.05 in SL (NSW) . *A. lenisquamis*
- Surface of scales with texture, the posterior edge rounded, the cteni strongly projecting; snout length 2.8–3.0 in HL; caudal-peduncle depth 1.45–1.75 in HL; caudal-fin length 3.95–4.8 in SL (NSW) . . . . . *A. nigrocirratus*
- 9. Eye large, 3.95–4.2 in HL; caudal fin long, 3.9–3.95 in SL; longest dorsal ray 1.4 in HL (New Caledonia) . . . . .  
. . . . . *A. magnoculus*
- Eye not as large, 4.55–7.0 in HL; caudal fin not long, 4.4–5.3 in SL; longest dorsal ray 1.45–1.8 in HL . . . . 10
- 10. Anal rays 58–59; dorsal rays 78–83; longest dorsal ray 1.8 in HL; caudal fin short, 4.7–5.3 in SL (3 specimens, Marquesas Islands) . . . . . *A. lateralis*
- Anal rays 53–57; dorsal rays 68–77; longest dorsal ray 1.45–1.7 in HL; caudal fin not short, 4.4–4.8 in SL . . 11
- 11. Dorsal rays 74–77; anal rays 56–57; head large, the length 3.85–3.95 in SL; body depth 2.45–2.55 in SL; caudal fin 4.4–4.45 in SL (Society Islands) . . . . . *A. auroculus*
- Dorsal rays 68–71; anal rays 53; head not large, the length 4.65–4.95 in SL; body depth 2.25–2.4 in SL; caudal fin 4.7–4.8 in SL (Society Islands) . . . . . *A. cyclurus*

*Aseraggodes auroculus* sp. nov.

Figure 2, Tables 1–4

*Holotype*. ROM 61358, 35.5 mm, Society Islands, Moorea, off NW coast, 17°31'0"S, 149°55'30"E, reef slope of coral rubble, with some live coral (including a few large heads of *Porites*), 18–24 m, rotenone,

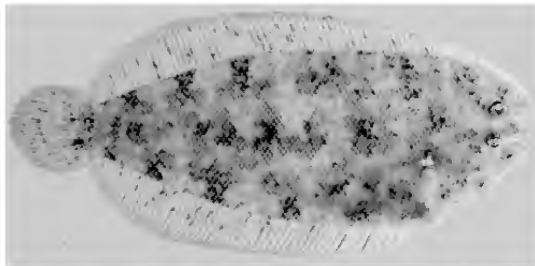


Figure 2. Holotype of *Aseraggodes auroculus*, ROM 61358, 35.5 mm, Moorea, Society Islands (R. Winterbottom).

R. Winterbottom and R. Mooi, 10 Dec 1989.

*Paratypes*. ROM 61357, 34.0 mm, Society Islands, Moorea, W side of pass off Maharepa about middle of its length, 17°29'24"S, 149°48'0"W, 15–18 m, steep slope with coral rubble, sand, and a 3-m wall, rotenone, R. Winterbottom and R. Mooi, 5 Dec 1989; BPBM 39690, 30.4 mm and USNM 381623, 29.8 mm, same data as holotype.

*Diagnosis*. Dorsal rays 74–77; anal rays 56–57; most dorsal and anal rays double branched; lateral-line scales 69–73, including 6–7 anterior to a vertical at upper end of gill opening; vertebrae 37–38; dorsal pterygiophores anterior to fourth neural spine 12; body depth 2.45–2.6 in SL; HL 3.85–3.95 in SL; eye diameter 4.55–4.9 in HL; upper eye overlapping a anterior two-thirds to three-fourths of lower eye; interorbital

Table 1. Dorsal Rays of South Pacific Species of *Aseraggodes*

	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
<i>A. auroculus</i>													1	1	1	1	
<i>A. bahamondei</i>				2	3	4	7	6	5	3							
<i>A. cyclurus</i>							1		1	1							
<i>A. lateralis</i>																1	2
<i>A. lenisquamis</i>	1	1		4	4	1		1	1								
<i>A. magnoculus</i>						1			1		1						
<i>A. melanostictus</i>													1	1			
<i>A. nigrocirratus</i>		2	1	1	2	1	2										
<i>A. normani</i>			1		1		1	2		2							
<i>A. pelvicus</i>										1							
<i>A. ramsaii</i>								1		1	1						
<i>A. whitakeri</i>										3	3	1	1	3	1		1

Table 2. Anal rays of South Pacific species of *Aseraggodes*

	46	47	48	49	50	51	52	53	54	55	56	57	58	59
<i>A. auroculus</i>											3	1		
<i>A. bahamondei</i>					1	2	8	10	5	3	1			
<i>A. cyclurus</i>								3						
<i>A. lateralis</i>													2	1
<i>A. lenisquamis</i>	2	2		1	2	5	1							
<i>A. magnoculus</i>						1	1	1						
<i>A. melanostictus</i>								1	1					
<i>A. nigrocirratus</i>		2	2	1	2		1	1						
<i>A. normani</i>					3	2	2							
<i>A. pelvicus</i>				1										
<i>A. ramsaii</i>		1		1	1									
<i>A. whitakeri</i>			1	1	2	2	5	2						

Table 3. Lateral-line scales of South Pacific species of *Aseraggodes*

	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88
<i>A. auroculus</i>											1		2		1															
<i>A. bahamondei</i>																	2	1	2	3	4	3	5	1	4	3	1	1		
<i>A. cyclurus</i>												1		1	1															
<i>A. lateralis</i>																					1	1			1					
<i>A. lenisquamis</i>				2		2	1	2		1	3	2																		
<i>A. magnoculus</i>													1	1			1													
<i>A. melanostictus</i>																					1	1								
<i>A. nigrocirratus</i>		1	2			1	2	1	2																					
<i>A. normani</i>										1		2	3		1															
<i>A. pelvicus</i>																							1							
<i>A. ramsaii</i>																												1	1	1
<i>A. whitakeri</i>																			1	1	2	3	1	1	2	1		1		

Table 4. Proportional measurements of type specimens of *Aseraggodes auroculus* as percentages of standard length

	Holotype		Paratypes	
	ROM 61358	USNM 381623	BPBM 39690	ROM 61357
Standard Length (mm)	35.5	29.8	30.4	34.0
Body depth	38.1	40.7	39.6	39.3
Body width	7.1	7.1	8.4	7.3
Head length	25.3	25.4	26.0	25.8
Snout length	8.6	9.2	8.2	8.8
Preorbital length	7.1	7.6	7.5	7.8
Eye diameter	5.5	5.6	5.3	5.7
Interorbital width	1.4	1.5	1.0	1.1
Upper-jaw length	8.7	8.8	8.9	8.8
Caudal-base depth	13.4	14.1	13.2	13.8
Predorsal length	6.2	6.1	6.3	5.9
Preal length	30.6	29.4	29.6	30.0
Prepelvic length	23.8	23.8	23.2	24.1
First dorsal ray	6.7	6.9	6.8	6.5
Longest dorsal ray	15.2	16.4	15.8	15.0
First anal ray	7.0	6.4	6.7	6.6
Longest anal ray	15.4	16.7	broken	15.1
Caudal-fin length	22.6	broken	22.7	22.6
Pelvic-fin length	10.2	10.6	9.7	9.5

space narrow, the vertical distance separating eyes about one-fourth to one-sixth eye diameter; no caudal peduncle; short fleshy cirri on ventral edge of head; lateral line aligned with ventral part of upper eye; longest dorsal ray 1.55–1.7 in HL; caudal fin rounded, its length 4.4–4.55 in SL; pelvic fins 2.4–2.7 in HL, the tip of longest ray reaching base of second or third anal ray; colour of ocular side in alcohol pale yellowish brown with 3 rows of large irregular blackish blotches, one dorsal, one ventral, and one midlateral; a few small dark spots on fin rays; blind side of body pale yellowish, the dark spots on rays faint.

*Description.* Dorsal rays 75 (74–77); anal rays 56 (56–57); dorsal rays branched except first 9 dorsal rays of holotype and first 19 of smallest paratype; anal rays branched; caudal rays 18, the middle 16 of holotype double-branched (middle 12–14 of paratypes double-branched); pelvic rays 5, branched except first; lateral-line scales 69 (71–73), including 6–7 anterior to a vertical at upper end of gill opening; scales above lateral line on ocular side to dorsal-fin base about 22; scales below

lateral line to anal-fin base about 24; vertebrae 37 (37–38); erisma (counted as the first dorsal pterygiophore) about twice as thick as remaining pterygiophores, its inner half narrowly branched; next 2 pterygiophores before tip of second neural spine; space between second and third neural spines with 6 pterygiophores; space between third and fourth neural spines with 3 pterygiophores; total of 12 dorsal pterygiophores anterior to fourth neural spine; ventroanterior margin of urohyal forming an angle of about 80°, the corner broadly rounded.

Body depth 2.6 (2.45–2.55) in SL; body width (thickness) 5.3 (4.7–5.75) in body depth; ventral profile of head posterior to mouth slightly convex; HL 3.95 (3.85–3.95) in SL; snout length 2.7 (2.6) in HL; eye diameter 4.6 (4.55–4.9) in HL; upper eye overlapping anterior two-thirds to three-fourths of lower eye; least vertical interorbital width 3.55 (2.75–3.35) in HL; upper end of gill opening on a horizontal passing about one-half eye diameter ventral to lower eye; no caudal peduncle (base of last two or three anal rays posterior to base of lowermost caudal ray); depth at base of caudal fin 1.9 (1.8–1.95) in HL.

Maxilla extending to below front edge of pupil, the upper-jaw length (measured on blind side) 2.9 (2.9–2.95) in HL; blind side of upper and lower jaws with a dense band of villiform teeth (difficult to see because just medial to a labial fold); no teeth on ocular side of jaws; tubular anterior nostril of ocular side membranous, just above upper lip, anterior to upper edge of lower eye, slightly tapering, reaching a little posterior to front edge of eye when laid back, its length about three-fourths eye diameter; posterior nostril an oblique slit in labial groove directly in front of dorsal half of lower eye; anterior nostril of blind side a more slender, slightly tapering, membranous tube above about middle of upper lip; posterior nostril of blind side a shorter, broader membranous tube posterior and slightly dorsal to anterior nostril (internarial distance about three-fourths eye diameter).

Scales ctenoid on both sides (except those of lateral line partially embedded); scales of ocular side of body with 6–9 cteni; about 2 rows of scales in interorbital space, with about another 5 rows extending onto medial and anterior part of each eye; scales on ocular side of head progressively smaller anteriorly and ventrally with fewer cteni, replaced on snout by fleshy papillae; scales on blind side of head anterior to a demarcation just posterior to end of jaws replaced by a dense zone of fleshy papillae that are progressively longer anteriorly, about 15 visible on ventral edge of head posterior to mouth (long for papillae, but too stout and short to call cirri). Lateral line straight on both sides along middle of body, projecting on ocular side toward ventral edge of upper eye; lateral line of blind side replaced by a row of sensory papillae on head (differentiated from surrounding papillae by a narrow papilla-free zone on each side), which curves ventrally at front of head; supratemporal branch of lateral line on blind side of head clearly visible as a similar row of low sensory papillae just below basal



sheath of scales, becoming faint at end of about anterior third of body.

Each dorsal and anal ray with a thin lengthwise membranous ridge, narrowing distally; ridges progressively less developed posteriorly; small scales and papillae extending out on ridges of both sides of about first 20 dorsal rays, making edges of membranous ridges jagged; about basal fourth of caudal fin with progressively smaller scales on both sides to at least three-fourths length of fin.

Origin of dorsal fin anterior to lower edge of upper eye, the predorsal length 4.1 (4.15–4.4) in HL; first dorsal ray (only the tip free) 3.8 (3.7–3.95) in HL; longest dorsal ray 1.65 (1.55–1.7) in HL; origin of anal fin below base of 20th dorsal ray, slightly posterior to a vertical at end of opercular membrane, the preanal length 3.3 (3.35–3.4) in SL; length of first anal ray 3.6 (3.9–3.95) in HL; longest anal ray 1.65 (1.5–1.7) in HL; caudal fin rounded, 4.45 (4.4–4.45) in SL; pelvic fin bases adjacent on ventral edge of body, third and fourth pelvic rays longest, reaching to base of second or third anal ray, 2.5 (2.4–2.7) in HL; anus anterior to first anal ray; genital papilla dorsoposterior to anus, not connected by membrane to ocular-side pelvic fin.

Colour of ocular side of holotype when fresh: brownish yellow with numerous whitish blotches about half eye diameter in size, many interconnected; three rows of very irregular, large, blackish blotches, the dark pigment on scale edges, or isolated scales entirely black; a small squarish white spot behind upper end of gill opening; eyes golden with faint blackish bands, partly rimmed in black; fins with translucent membranes and brownish yellow rays, some with 1 or 2 blackish spots; scaly basal part of caudal fin coloured like body.

Colour of ocular side of holotype in alcohol: pale yellowish brown with 3 rows of large irregular blackish blotches, one dorsal, one ventral, and one midlateral; a few small dark spots on fin rays; blind side of body pale yellowish, the dark spots faint.

**Etymology.** The species name *auroculus* is from the Latin *aurum* for gold and *oculus* for eye, in reference to the bright golden colour of the eyes.

**Remarks.** The four specimens of this species were collected in 1989 off Moorea in two rotenone stations from steep sloping bottoms dominated by coral rubble at depths of 15–24 m. They were deposited in the Royal Ontario Museum with a tentative identification of *Aseraggodes melanostictus* (Peters), the name often given to specimens of soles of this genus with an ocular-side colour pattern of large blackish blotches. Although sharing the same number of dorsal rays, vertebrae, and dorsal pterygiophores with *A. melanostictus*, *A. auroculus* is easily distinguished by a higher count of anal rays, fewer lateral-line scales (Tables 2 and 3), and having branched instead of unbranched dorsal and anal fin rays. It also appears to be a much smaller species. The two known specimens of

*A. melanostictus* measure 74 and 86.5 mm SL.

*Aseraggodes auroculus* is more closely related to *A. cyclurus*, also collected from the Society Islands. One rotenone station resulted in a specimen of both species. The two are separated by dorsal- and anal-ray counts and differences in body depth, eye size, and length of the caudal fin (see Key). Also, *A. cyclurus* seems to be a larger species. The three Society Islands specimen range from 61.5 to 73.3 mm SL, compared to 29.8–35.5 mm for the four type specimens of *auroculus*. The 34.0 mm paratype of *A. auroculus* is a fully mature female.

The photograph taken of the holotype of *Aseraggodes auroculus* (Fig. 2), shows a broad interorbital space, about three-fourths the diameter of the lower eye. The interorbital width of the preserved specimen is only one-fourth the eye diameter. The same shrinkage of the interorbital space was noted for one specimen of *A. lenisquamis* (see description below).

#### *Aseraggodes bahamondei* Randall and Meléndez, 1987

Figures 3–5, Tables 1–3

*Aseraggodes bahamondei* Randall and Meléndez, 1987: 99, figs 1–3.

**Material examined.** See Randall and Meléndez (1987).

**Type locality.** Easter Island.

**Diagnosis.** Dorsal rays 65–71; anal rays 50–56; dorsal and anal rays branched, except in juveniles; lateral-line scales 75–86; 1–4 pores beneath many scales peripherally on ocular side of

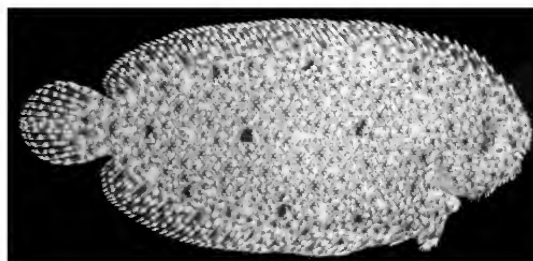


Figure 4. Paratype of *Aseraggodes bahamondei*, BPBM 14790, 68.3 mm SL, Lord Howe Island.

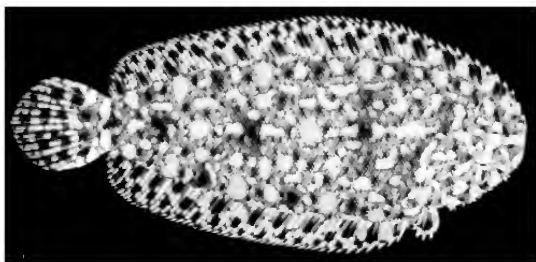


Figure 3. Paratype of *Aseraggodes bahamondei*, BPBM 30851, 46.9 mm SL, Easter Island.

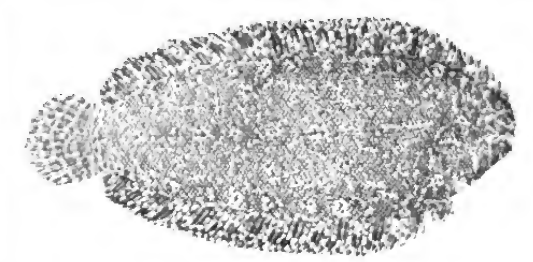


Figure 5. Holotype of *Aseraggodes bahamondei*, BPBM 6610, 149.3 mm SL, Easter Island.



body; vertebrae 39–40; dorsal pterygiophores anterior to fourth neural spine 7–8; body depth 2.3–2.5 in SL; HL 3.8–4.55 in SL (relatively longer in small individuals); upper lip not overlapping lower lip when mouth closed; eye diameter 5.8–6.8 in HL; upper eye varying from slightly anterior to one-half eye diameter before lower eye; interorbital space 6.5–9.55 in HL; tubular anterior nostril of ocular side not reaching edge of lower eye when laid back; prominent lappet-like cirri on ventral edge of head; caudal peduncle present, its length 11.0–15.5 in HL; lateral line aligned with ventral half of upper eye; dorsal and anal rays short, the longest dorsal ray 1.9–2.15 in HL; small scales extending out on membranous ridge of dorsal and anal rays, but no cirri at free edge of ridges; caudal fin rounded, 4.0–5.1 in SL; origin of ocular-side pelvic ray slightly anterior to blind-side fin; third pelvic ray longest, reaching to or a little beyond base of second anal ray, 2.8–3.2 in HL; pale brown with dark-edged white spots and 3 rows of black spots, these markings relatively smaller and more irregular, in general, with growth. Largest specimen, 156 mm SL.

**Remarks.** Currently known only from Easter Island and Lord Howe Island, but is likely to occur at some intermediate southern subtropical islands such as Pitcairn, Rapa, Kermadec Islands, or Norfolk Island. Collected from sand at depths of 2–25 m. This species is unique in having the highest vertebral count and lowest number of anterior dorsal pterygiophores. It also seems to reach the largest size of species of the genus. Randall and Meléndez demonstrated the toxicity of the milky secretion exuded by this species when threatened, presumably from the small pores beneath scales near the edge of the ocular side of the body.

*Aseraggodes cyclurus* sp. nov.

Figure 6, Tables 1–3, 5

**Holotype.** BPBM 8105, 73.3 mm, Society Islands, Tahiti, Papara, Teavaraa Pass, SE side, sand at entrance to cave, 27.5 m, rotenone, J.E. Randall, 21 Sep 1967.

**Paratypes:** USNM 379462, 70.2 mm, same data as holotype; ROM 61359, 61.5 mm SL, Society Islands, Moorea, W side of pass off Maharepa about middle of its length, 17°29'24"S, 149°48'0"W, 15–18 m, steep slope with coral rubble, sand, and 3-m wall, rotenone, R. Winterbottom and R. Mooi, 5 Dec 1989.

**Diagnosis.** Dorsal rays 68–71; anal rays 53; most dorsal and

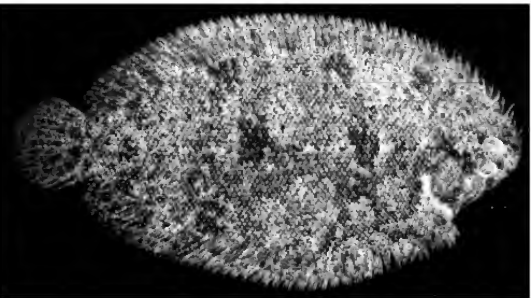


Figure 6. Holotype of *Aseraggodes cyclurus*, BPBM 8105, 73.3 mm SL, Tahiti, Society Islands.

anal rays double branched; lateral-line scales 70–73 (including 6–7 anterior to a vertical at upper end of gill opening); vertebrae 36–37; dorsal pterygiophores anterior to fourth neural spine 10–11; body depth 2.25–2.4 in SL; HL 4.65 (4.7–4.95) in SL; eye diameter 4.65–4.9 in HL; upper eye overlapping about anterior half of lower eye; interorbital space narrow, the vertical distance separating eyes about three-fourths eye diameter; no caudal peduncle; no prominent cirri on ventral edge of head; lateral line aligned with ventral edge of upper eye; longest dorsal ray 1.45–1.6 in HL; caudal fin rounded, its length 4.7–4.8 in SL; pelvic fins 2.2–2.4 in HL, the tip of longest ray reaching base of third anal ray; ocular side mottled brown, the scale edges dark brown to black; large irregular blackish blotches, the most prominent comprising 4 below base of dorsal fin, 3 on lateral line, and 2 above posterior half of anal fin.

**Description.** Dorsal rays 71 (68–70); anal rays 53; dorsal rays double-branched except first 19 (first 21 and 25 of paratypes); anal rays double-branched except first 5 and 9 rays of paratypes; caudal rays 18, all branched, the middle 16 double-branched; pelvic rays 5, all branched; lateral-line scales on ocular side 73 (70–72), including 6–7 anterior to a vertical at upper end of gill opening; scales above lateral line on ocular side to dorsal-fin base about 24; scales below lateral line to anal-fin base about 27; vertebrae 37 (36–37); erisma (counted as the first dorsal pterygiophore) about twice as thick as remaining pterygiophores, its inner half narrowly branched; next 2 pterygiophores before tip of second neural spine; space between second and third neural spines with 5 pterygiophores; space between third and fourth neural spines with 2 (2–3) pterygiophores; total of 10 (10–11) dorsal pterygiophores anterior to fourth neural spine; ventroanterior margin of urohyal forming an angle of about 80°, the corner well-rounded.

Body depth 2.25 (2.25–2.4) in SL; body width (thickness) 5.65 (4.6–6.0) in body depth; ventral profile of head posterior to mouth nearly straight; HL 4.65 (4.7–4.95) in SL; snout length 2.7 (2.6) in HL; eye diameter 4.9 (4.65–4.7) in HL; least vertical interorbital width 8.0

Table 5. Proportional measurements of type specimens of *Aseraggodes cyclurus* as percentages of standard length

	Holotype	Paratype	Paratype
	BPBM 8105	ROM 61359	USNM 379462
Standard Length (mm)	73.3	61.5	70.2
Body depth	44.7	44.6	42.1
Body width	7.9	9.7	7.0
Head length	21.6	21.4	20.2
Snout length	8.0	8.3	7.8
Preorbital length	7.8	7.5	7.7
Eye diameter	4.4	4.6	4.3
Interorbital width	2.7	2.7	2.8
Upper-jaw length	8.2	8.1	8.1
Caudal-base depth	13.8	14.6	14.3
Predorsal length	5.3	5.5	5.4
Preanal length	25.3	24.1	25.7
Prepelvic length	19.3	18.2	18.5
First dorsal ray	3.9	4.4	4.2
Longest dorsal ray	14.4	15.4	14.6
First anal ray	6.6	6.4	6.7
Longest anal ray	15.0	15.6	15.7
Caudal-fin length	21.2	22.7	22.6
Pelvic-fin length	9.6	9.5	9.7

(7.2–7.95) in HL; a vertical at posterior edge of upper eye (edge of dark eyeball) passing approximately through middle of lower eye; upper end of gill opening on a horizontal passing about one-half eye diameter ventral to lower eye; no caudal peduncle (base of lowermost caudal ray ending above base of last anal ray); depth of body at base of caudal fin 1.55 (1.4–1.45) in HL.

Snout not overlapping lower jaw when mouth closed; maxilla extending slightly posterior to a vertical at front edge of lower eye, the upper jaw length (blind side) 3.65 (2.5–2.65) in HL; blind side of upper and lower jaws with a dense band of slender, inward-projecting, slightly curved teeth up to about 7 rows; no teeth on ocular side of jaws; anterior nostril a tapering membranous tube anterior to upper edge of lower eye, just reaching anterior edge of eyeball when laid back, its length nearly equal to eye diameter; posterior nostril an oblique slit in labial groove directly in front of ventral part of lower eye; anterior nostril of blind side a short tapering membranous tube just above anterior third of upper lip; aperture of posterior nostril of blind side dorsoposterior to anterior nostril (internarial distance about equal to eye diameter), covered anteriorly with a flattened papilla.

Scales ctenoid on both sides (except those of lateral line partially embedded); scales of ocular side of body with 10–13 cteni; 3 rows of scales in interorbital space, with about another 6 rows extending onto medial half of each eye; scales on ocular side of head progressively smaller anteriorly and ventrally, the very small scales at front of snout without cteni; scales on blind side of head replaced anteriorly by small slender stout papillae on front of snout; a dense zone of small fleshy papillae ventral and adjacent to lower jaw on blind side and another adjacent to upper jaw, the latter not much broader than jaw width; anterior edge of snout and ventral edge of head with very fine cirri, none along edge of operculum at gill opening on either side. Lateral line straight on both sides along middle of body, projecting on ocular side toward ventral edge of lower eye; lateral-line of blind side obscure on head in zone of papillae where it curves well dorsal to upper jaw to tip of snout; a supratemporal branch of lateral line on blind side of head faintly visible, beginning at front of snout, and continuing along base of dorsal fin to anterior body.

Dorsal and anal fins with a basal sheath of 2 to 3 rows of scales; small scales continuing out on rays and adjacent membrane on first 25 rays of dorsal fin of ocular side of holotype, those on rays on a thin membranous ridge basally on each ray; only a few scales basally on first 7 rays of ocular side of anal fin; scales basally on rays of blind side except for last 19 rays of dorsal fin and last 17 of anal fin; small cirri projecting from edge of membranous ridge of anterior dorsal and anal rays of ROM paratype (but not apparent on Bishop Museum specimens); about basal third of caudal fin with scales on both sides; tiny, well-spaced, isolated scales still with cteni, on each side of rays posteriorly to within outer fourth of fin.

Origin of dorsal fin anterior to lower edge of upper eye, the pre-dorsal length 4.85 (4.6) in HL; first dorsal ray (only the tip free) 6.55 (4.9) in HL; longest dorsal ray 1.75 (1.7) in HL; origin of anal fin below base of 20th dorsal ray and in line with posterior end of opercular membrane, the preanal length 3.95 (3.9) in SL; length of first anal ray 3.9 (3.7) in HL; longest anal ray 1.7 (1.6) in HL; caudal fin rounded, 4.8 (4.7) in SL; ocular-side pelvic fin on ventral edge of body, blind-side fin adjacent, both covered anteriorly by a basal band of small scales; third pelvic ray of each fin longest, reaching to base of third anal ray, 2.65 (2.55) in HL; anus ventroanterior to first anal ray; genital papilla on ocular side of base of first anal ray.

Colour of ocular side of holotype in alcohol pale tan, fins with pale yellowish rays and transparent membranes; no dark markings apparent.

Colour of holotype when fresh light brown, edges of the scales dark brown to black, with scattered small irregular pale blotches and smaller dark brown spots; large irregular blackish blotches in 3 rows: upper row of 4 blackish blotches along dorsal contour of body, middle row of

four blotches on lateral line, the first at origin of lateral line, the 2 middle blotches clearly largest on body; lower row of 4 blotches below base of anal fin, less distinct than other blotches; blind side of body whitish; opercular membrane pale; fin rays mottled brown to dark brown, the membranes pale.

**Etymology.** Named *cyclurus* from the Greek for the nearly circular caudal fin.

**Remarks.** This species is described from three specimens, two from sand at the entrance to a cave in Tahiti at a depth of 27.5 m, and the third on a steep rubble and sand slope in 15–18 m in a pass at Moorea.

A fourth specimen, BPBM 20864, 56.6 mm, collected at Budd Reef, Ringgold Isles, Fiji, in 11–26 m with rotenone by B.A. Carlson and M. Gawel on 14 Apr 1973, is provisionally identified as *Aseraggodes cyclurus*. The head and body were preserved in a curve, so it is difficult to make accurate proportional measurements, no photograph or colour notes were taken, and the colour has largely faded. The specimen has 70 dorsal rays, those posterior to 18th ray double-branched; 52 anal rays, those posterior to third ray double-branched, 74 lateral-line scales, 36 vertebrae, and 11 dorsal pterygiophores anterior to the fourth neural spine.

*Aseraggodes cyclurus* seems most closely related to *A. heraldi* Randall and Bartsch, described from two specimens, 38.5 and 47 mm SL, from the Marshall Islands. The two species share the following characters: no caudal peduncle, same vertebral count, lack of prominent cirri along the ventral edge of the head, scales extending onto anterior dorsal and anal rays beyond the basal scaly sheath, and many double-branched rays of the dorsal and anal fins. They differ slightly in the number of dorsal rays (70–73 for *A. cyclurus* vs 75 for *A. heraldi*) and anal rays (51 and 52 for *A. cyclurus* vs 57 and 58 for *A. heraldi*) and the number of dorsal pterygiophores before the fourth neural spine, 10 for *A. cyclurus* (11 for the non-type from Fiji), compared to 12 for *A. heraldi*. The difference in snout length is the only difference in proportional measurements that seems great enough to be beyond individual variation, given the difference in size of the specimens under comparison. The snout length of *A. heraldi* is longer, 8.1–8.2 in SL, compared to 6.8–6.9 for *A. cyclurus*. Also significant is the more extensive area of papillae anteriorly on the blind side of the snout of *A. heraldi*; the entire snout dorsal to the straight anterior part of the upper jaw is densely covered with small papillae. In *A. cyclurus* there is only a zone of papillae adjacent to the jaw that is not much wider than the jaw. There is also a difference in the basic colour pattern of the two species. The dark blotches in the three basic rows on the body are more numerous, and their relative size smaller in *A. heraldi*.

### *Aseraggodes lateralis* sp. nov.

Figures 7, 8, Tables 1–3, 6

**Holotype.** BPBM 10992, 64.2 mm, Marquesas Islands, Ua Huka, W side, small bay 0.4 miles NE of Motu Takatai, N side of bay in 4.5–9 m, rotenone, J.E. Randall, J.R. Haywood, and R.M. McNair, 7 May 1971.

**Paratypes.** BPBM 12757, 27.8 mm, Marquesas Islands, Nuku Hiva, Sentinelle de l'Est, W side, steep rocky slope with no visible sand, 23 m, quinaldine, J.E. Randall and D.B. Cannoy, 17 May 1971; USNM

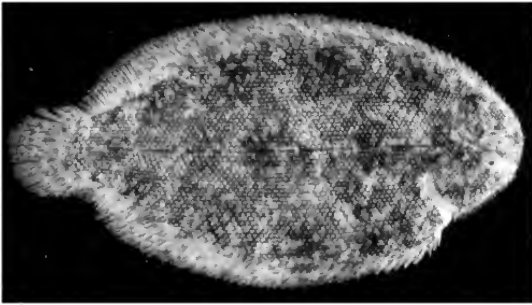


Figure 7. Holotype of *Aseraggodes lateralis*, BPBM 10992, 64.2 mm SL, Ua Huka, Marquesas Islands.

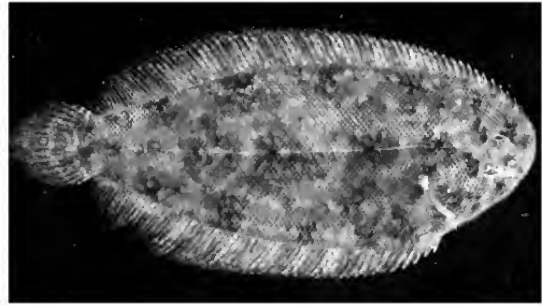


Figure 8. Paratype of *Aseraggodes lateralis*, BPBM 12757, 27.8 mm SL, Nuku Hiva, Marquesas Islands.

Table 6. Proportional measurements of the type specimens of *Aseraggodes lateralis* as percentages of standard length

	Holotype BPBM 10992	Paratype BPBM 12757	Paratype U S N M 382053
Standard Length (mm)	64.2	27.8	37.7
Body depth	50.2	41.6	42.0
Body width	8.1	7.2	7.9
Head length	22.2	22.4	23.8
Snout length	7.5	7.5	7.4
Preorbital length	6.5	6.4	6.6
Eye diameter	3.8	4.2	3.9
Interorbital width	2.9	2.1	2.0
Upper-jaw length	7.0	7.1	6.7
Caudal-base depth	15.3	13.9	12.3
Predorsal length	4.5	4.2	4.9
Preal length	29.7	28.6	29.2
Prepelvic length	25.2	24.1	24.6
First dorsal ray	4.6	4.3	5.3
Longest dorsal ray	13.3	14.0	14.3
First anal ray	7.3	6.8	7.4
Longest anal ray	13.7	14.3	14.4
Caudal-fin length	19.0	21.4	20.9
Pelvic-fin length	7.8	8.0	7.9

392053, 37.7 mm, Marquesas Islands, Fatu Hiva, Hanavave Bay, N side, 20 m, rotenone, J.L. Earle, L.A. Rocha, and W. Robbins, 23 Aug 2003.

**Diagnosis.** Dorsal rays 77–78; anal rays 58–59; lateral-line scales 78–83; vertebrae 37–38; dorsal pterygiophores anterior to fourth neural spine 12; body depth 2.0–2.4 in SL; HL 3.9–4.15 in SL; eye diameter 6.1–6.35 in HL; upper eye from directly above lower eye to overlapping anterior two-thirds of lower eye; interorbital space equal to one-half to three-fourths eye diameter; no caudal peduncle; upper lip not overhanging lower jaw when mouth closed; very fine cirri on ventral edge of head; lateral line aligned with ventral third of upper eye; longest dorsal ray 1.8 in HL; caudal fin rounded to slightly pointed, its length 4.7–5.25 in SL; longest pelvic ray 3.1–3.2 in HL, the tip reaching base of second anal ray; ocular side mottled brown; scale edges dark brown to black; large irregular blackish blotches, the most prominent comprising 4 below base of dorsal fin, 3 on lateral line, and 2 above posterior half of anal

fin; lateral line as a broken black line.

**Description.** Dorsal rays 77, the first 15 branched, remaining rays double-branched; anal rays 58 (59), all double branched; caudal rays 18 (uppermost and lowermost rays branched, the middle 16 double branched; pelvic rays 5, all branched; lateral-line scales 78 (79–83), including 7–8 anterior to a vertical at upper end of gill opening; scales above lateral line on ocular side to dorsal-fin base about 28; scales below lateral line to anal-fin base about 29; vertebrae 37 (38); erisma (counted as the first dorsal pterygiophore) nearly 3 times thicker than remaining pterygiophores, its inner three-fourths narrowly branched; next 2 pterygiophores before tip of second neural spine; space between second and third neural spines with 6 pterygiophores; space between third and fourth neural spines with 3 pterygiophores (total of 12 dorsal pterygiophores anterior to fourth neural spine); ventro-anterior margin of urohyal forming angle of about 80°, the corner strongly rounded.

Body oval and deep for genus, the depth 2.0 (2.35–2.4) in SL; body thin, the width 6.2 (5.7–5.8) in body depth; ventral profile of head posterior to mouth slightly convex; HL 4.5 (4.45–4.6) in SL; snout length 2.95 (2.95–3.0) in HL; eyes small, the eye diameter 5.85 (5.35–5.6) in HL; upper eye of holotype directly above lower (overlapping about anterior two-thirds of lower eye in paratypes); least vertical interorbital space 7.65 (10.7–10.9) in HL; upper end of gill opening at level of ventral edge of lower eye; no caudal peduncle (base of lowermost caudal ray ending above base of last anal ray); depth of body at base of caudal fin 1.45 (1.6–1.75) in HL.

Front of upper lip not overlapping lower jaw when mouth closed; maxilla extending to a vertical at anterior fourth of lower eye, the upper jaw length (blind side) 3.2 (3.15–3.25) in HL; blind side of jaws with a dense band of slender, inward-projecting, slightly curved teeth nearly the full length of each jaw, up to about 6 rows at broadest place; anterior nostril a tapering tube before upper edge of lower eye, reaching anterior edge of eye when laid back, its length about three-fourths eye diameter; posterior nostril an oblique slit in labial groove directly in front of ventral part of lower eye; anterior nostril of blind side a short tapering membranous tube just above anterior third of upper jaw; posterior nostril of blind side dorsoposterior to anterior nostril; intermarial distance about equal to eye diameter.

Scales of both sides ctenoid (except cycloid on lateral line and partially embedded), usually with 10 cteni (a few with 11 or 12); 4 rows of scales in interorbital space, with small scales extending broadly onto median and anterior edge of eyes (apparently lost in some); scales progressively shorter anteriorly on head and with fewer cteni (front of snout with very small scales without cteni, but not in the form of little papillae or tubercles); anterior edge of snout and ventral edge of head with a row very fine cirri (especially fine anteriorly on

snout); no cirri along edge of operculum; opercular membrane in form of a short triangle near upper end of gill opening. Lateral line straight on both sides along middle of body, on ocular side aligned with ventral third of upper eye; an indistinct supratemporal branch of lateral line on blind side of head, continuing faintly anteriorly on body along base of dorsal fin.

Dorsal and anal fins with a basal sheath of 2 to 3 rows of scales; ocular side with small scales continuing a short distance out on rays and adjacent membrane on first 31 rays of dorsal fin of ocular side of holotype, and on the first 8 rays of ocular side of anal fin; scales extending out on rays of dorsal and anal rays of blind side except for last 21 rays of dorsal fin and last 33 of anal fin; a thin lengthwise membranous scaly ridge basally on anterior dorsal and anal rays of both sides, progressively shorter posteriorly; about basal third of caudal fin with scales on both sides, and well-spaced tiny scales, still with cteni, continuing on each side of rays about half way out in fin.

Origin of dorsal fin anterior to lower edge of upper eye, the predorsal length 4.95 (4.45–4.65) in HL; first dorsal ray 4.85 (4.15–5.2) in HL; longest dorsal ray 1.65 (1.5–1.55) in HL; origin of anal fin below base of 20th dorsal ray and in line with posterior end of operculum, the preanal length 3.35 (3.45–3.5) in SL; anus anterior to first anal ray; genital papilla dorsoposterior to anus; first anal ray 3.05 (2.95–3.3) in HL; longest anal ray 1.6 (1.5–1.55) in HL; caudal fin rounded to slightly pointed, 5.25 (4.7–4.8) in SL; pelvic fins close together anteriorly on ventral edge of body, their origins adjacent; third pelvic ray of each fin longest, reaching base of third anal ray, 2.85 (2.75–2.8) in HL.

Colour of ocular side in alcohol light yellowish brown with scattered irregular brown blotches of variable size, the most conspicuous in 3 rows: one below base of dorsal fin, one following lateral line, and one just above anal fin; blind side uniform light yellowish brown; fins pale with a few faint small brown spots basally in dorsal and anal fins.

Colour of ocular side of holotype when fresh: light brown with small irregular pale and dark brown blotches; scale edges dark brown to black; large irregular blackish blotches containing small pale spots in 3 rows, dorsal, ventral, and along lateral line; lateral line clearly evi-

dent as a broken black line; posterior edge of operculum broadly white; eyes pale with radiating dark lines on dorsal half of iris; scaled basal part of fins coloured like body; remaining part of fins pale with small dark blotches and a few larger ones along base.

**Etymology.** Named *lateralis* from the Latin word with the same meaning in English, in reference to the distinct pigmented lateral line in life.

**Remarks.** The holotype was collected from rock and sand bottom of a protected bay, but the habitat of the smallest paratype was unexpected. It was taken from a steep rocky slope with no obvious sand during the day. Species of *Aseraggodes* are typically found on sedimentary bottoms, at least by day, and they are usually buried during daylight hours.

The smallest paratype of *Aseraggodes lateralis* is in poor condition with the fins badly eroded, a result of long retention in isopropanol of insufficient concentration. A comparison of the figures of the holotypes of *Aseraggodes lateralis* and *A. cyclurus* reveals similarity in body and fin morphology and in colour pattern. Both species have 37 vertebrae and nearly the same structure of the fins. *Aseraggodes cyclurus* differs in having higher dorsal, anal, and lateral-line scale counts (see Tables 1–3), extremely small cirri on the ventral edge of the head, and small slender tubercles instead of scales anteriorly on the blind side of the head.

The 37.7-mm paratype is a mature female. An x-ray revealed that it had eaten two gastropods with intact shells 1.7 and 1.9 mm long.

#### *Aseraggodes lenisquamis* sp. nov.

Figure 9, Tables 1–3, 7

*Aseraggodes* sp.—Kuitert, 1993: 391, upper fig. (central to south-

Table 7. Proportional measurements of type specimens of *Aseraggodes lenisquamis* as percentages of standard length

	Holotype			Paratypes				
	NMV A 19646	NMV A 25543	NSMT P 70086	AMS 1.27047	BMNH 4.10.26.4	CAS 221846	BPBM 39610	NMV A 25543
Standard Length (mm)	102.0	64.5	69.0	73.0	77.5	78.0	82.0	82.5
Body depth	39.4	38.6	40.6	37.8	41.1	41.3	41.2	39.9
Body width	7.2	7.4	7.5	7.8	7.8	7.5	7.8	7.3
Head length	20.3	19.9	20.6	20.4	20.8	20.3	21.1	20.9
Snout length	8.0	8.1	8.3	8.2	8.4	8.3	8.6	8.3
Preorbital length	6.4	6.4	6.5	6.4	6.7	6.4	6.2	6.1
Eye diameter	4.1	4.0	4.5	4.2	3.9	4.1	3.7	3.8
Interorbital width	2.0	1.9	1.5	2.8	2.6	2.5	2.4	2.7
Upper-jaw length	5.9	6.2	6.3	5.9	6.4	6.3	6.1	6.5
Caudal-base depth	14.9	15.5	16.2	15.3	15.2	14.9	14.5	15.6
Predorsal length	4.5	5.0	4.4	4.5	4.9	5.0	5.1	4.7
Preanal length	26.1	25.2	24.7	26.2	25.7	25.6	26.2	26.4
Prepelvic length	17.8	18.3	18.3	18.7	18.7	17.7	19.4	19.0
First dorsal ray	6.7	5.6	6.1	5.8	6.4	6.5	6.7	6.3
Longest dorsal ray	11.8	11.9	12.0	12.3	11.7	11.5	11.6	11.8
First anal ray	7.3	7.6	7.0	8.2	8.1	7.8	7.2	7.4
Longest anal ray	12.1	11.9	11.6	12.6	11.6	11.5	11.7	11.8
Caudal-fin length	21.8	21.9	21.0	21.6	20.8	19.8	19.9	20.9
Pelvic-fin length	9.8	10.9	9.9	11.1	10.7	10.2	10.5	10.5





Figure 9. Holotype of *Aseraggodes lenisquamis*, NMV A 19646, 102 mm, NSW.

ern NSW).

**Holotype.** NMV A 19646, 102 mm, Australia, NSW, Sydney Harbor, Camp Cove (33°50'S, 151°17'E), 4 m, hand net, R.H. Kuiter, 17 Jan 1985.

**Paratypes.** NMV A 3607, 65 mm, Australia, NSW, Bermagui, Horseshoe Bay, 36°25'S, 150°4'E, 10 m, hand net, R.H. Kuiter, 24 Jan 1984; NMV A 5827, 88 mm, same locality as preceding, 4–10 m, hand net, R.H. Kuiter, 30 Jan 1984; NMV A 25543-002, 2: 64.5–82.5 mm, BPBM 39610, 82 mm, CAS 221846, 78 mm, NSMT P 70086, 69 mm, BMNH 2004.10.26.4, 77.5 mm, USNM 380210, 68 mm, all with same data as holotype; AMS I.27047-001, 73 mm, NSW, Jervis Bay, Hare Bay, 35°3'S, 150°44'E, 6 m, beam trawl, F.R.I. Jervis Bay study, 28 Oct 1986; AMS 27063-013, 65 mm, NSW, Jervis Bay, Hare Bay, 35°0'S, 150°45'E, 2–7 m, J. Bell (State Fisheries), Dec 1986; AMS I.28514-002, 79 mm, NSW, Jervis Bay, Darling Road, 35°3'S, 150°44'E, 5 m, beam trawl, J. Bell and party, 28 Sep 1988.

**Diagnosis.** Dorsal rays 62–70; anal rays 46–52; dorsal and anal rays branched; lateral-line scales 62–68, including 8–9 anterior to a vertical at upper end of gill opening; vertebrae 36–38; dorsal pterygiophores anterior to fourth neural spine 8–9; body depth 2.4–2.65 in SL; head short, its length 4.75–5.05 in SL; eye diameter 4.6–5.7 in HL; upper eye overlapping about anterior one-third to one-half of lower eye; interorbital space variable in width, the vertical distance separating eyes 7.3–13.7 in HL; no caudal peduncle; lappet-like cirri on ventral edge of head, but not on front of snout; numerous cirri on opercular edge of gill opening on both sides; dense cirri over much of ventral part of head; exposed surface of scales overlaid with soft tissue; only tips of cirri visible at scale margins, capped with soft tissue; lateral-line scales with fleshy cirri, often one above and one below pore (cirri better developed on ocular than blind side); scattered other scales with a slender fleshy cirrus, often one from each corner of scale; membranous ridges of both sides of dorsal and anal rays with a conspicuous fringe of cirri, some of which are bifid; lateral line aligned with upper eye; longest dorsal ray 1.65–1.8 in HL; caudal fin rounded, its length 4.6–5.05 in SL; pelvic fins short, 1.8–2.2 in HL, the tip of longest ray reaching base of second anal ray; ocular side light brown, with scattered small dark brown blotches; rays of fins with small dark brown spots. Largest specimen, 102 mm SL.

**Description.** Dorsal rays 69 (62–70); anal rays 51 (46–52); dorsal and anal rays branched, most double-branched in large specimens; caudal

rays 18, branched, the middle 16 double-branched; pelvic rays 5, double-branched; lateral-line scales on ocular side 67 (62–68), including 8–9 anterior to a vertical at upper end of gill opening; scales above lateral line on ocular side to dorsal-fin base about 21; scales below lateral line to anal-fin base about 23; vertebrae 37 (five paratypes with 37, two with 36, and one with 38); dorsal pterygiophores anterior to fourth neural spine 9 (8–9); only the erisma (counted as the first dorsal pterygiophore before tip of second neural spine) about twice as thick as remaining pterygiophores, its inner third narrowly branched; next 5 (5–6) pterygiophores in space between second and third neural spines; space between third and fourth neural spines with 3 (2–3) pterygiophores; total pterygiophores before fourth neural spine 9 (five paratypes with 9, and four with 8); ventroanterior margin of urohyal forming an angle of about 55°, the corner only slightly rounded.

Body depth 2.55 (2.4–2.65) in SL; body width 5.45 (4.85–5.45) in body depth; ventral profile of head posterior to mouth nearly straight; head short, its length 4.85 (4.75–5.05) in SL; snout length 2.55 (2.45–2.5) in HL; eye diameter 4.95 (4.6–5.7) in HL; least vertical interorbital width 10.2 (7.3–13.7) in HL; upper eye overlapping anterior one-third to one-half of lower eye; upper end of gill opening on a horizontal passing about an eye diameter ventral to lower eye; no caudal peduncle (base of lowermost caudal ray ending above base of last anal ray); depth of body at base of caudal fin 1.35 (1.25–1.45) in HL.

Front of upper lip not overlapping lower lip when mouth closed; maxilla extending to below anterior margin of pupil, the upper jaw length (blind side) 3.45 (3.25–3.45) in HL; blind side of upper and lower jaws with a dense band of slender, inward-projecting, slightly curved teeth in a maximum of about 8 rows; no teeth on ocular side of jaws; anterior nostril a short membranous tube, tapering very little, anterior to upper edge of lower eye, and not reaching edge of eye when laid back; posterior nostril a slit in labial groove in front of upper half of lower eye; anterior nostril of blind side a membranous tube above anterior third of upper lip; posterior nostril of blind side dorso-posterior to anterior nostril; internarial distance about two-thirds eye diameter.

Surface of scales smooth, the ridges of ctenii covered with cutaneous tissue; free margin of scales angular (though posterior end not acutely pointed); only tips of ctenii of scales visible at scale margin (up to 14 on holotype), each covered with soft tissue; 2 (2–4) rows of scales in interorbital space, with another 2–3 rows extending medially and anteriorly onto eyes; no pores detected beneath scales on ocular side of body; scales on ocular side of head progressively smaller anteriorly, replaced at front of snout and ventrally on head with band of dense cirri nearly eye diameter in width; cirri at front edge of snout very small, those of ventral edge of head longer and more lappet-like, the longest nearly pupil diameter in length, a few branched at tips; a broader band of dense cirri anteriorly on blind side of head, around mouth, and extending in a zone along supratemporal branch of lateral line, which continues, progressively less distinct, onto about anterior half of body; band of cirri at edge of operculum on both sides, a dense fringe along gill opening; lateral-line scales with cirri, usually one above and one below the pore; scattered other scales with cirri, generally one at each corner; dorsal end of gill opening on a horizontal line passing about an eye diameter below lower eye. Lateral line straight midlaterally on both sides, projecting on ocular side toward upper eye.

Dorsal and anal fins with a basal sheath of 2 rows of scales; dorsal and anal rays on both sides with a fleshy lengthwise ridge bearing a fringe of prominent cirri; ridges on rays less developed posteriorly and with fewer cirri, especially on blind side; scales on basal half of caudal fin progressively smaller distally.

Origin of dorsal fin anterior to upper eye, the predorsal length 4.5 (4.0–4.65) in HL; first dorsal ray 3.0 (3.1–3.55) in HL; longest dorsal ray 1.7 (1.65–1.8) in HL; origin of anal fin below base of seventeenth

dorsal ray and slightly posterior to end of opercular membrane, the preanal length 3.85 (3.8–4.05) in SL; length of first anal ray 2.8 (2.5–2.95) in HL; longest anal ray 1.7 (1.6–1.8) in HL; caudal fin rounded, 4.6 (4.6–5.05) in SL; anus directly before first anal ray, preceded by fan-like semicircle of plicate tissue; genital papilla on ocular side of anus, its length nearly three-fourths eye diameter in holotype; bases of pelvic fins adjacent anteriorly, diverging posteriorly, the ocular-side fin a little before blind-side fin; pelvic fins not joined by membrane or to genital papilla; third pelvic ray of each fin longest, reaching to base of second anal ray, 2.05 (1.85–2.0) in HL.

Colour of ocular side of holotype in alcohol light brown with many small dark brown blotches, some stellate or cross-shaped; fins pale yellowish with small dark brown spots along rays, most spots coinciding with one or a clump of cirri (see below).

**Etymology.** This species is named *lenisquamis* from the Latin *lenis* for soft or smooth and *squama* for scale, in reference to the distinctive scale structure. The ctenii of the scales are nearly covered by soft epidermal tissue, with only the tips exposed at the scale margin.

**Remarks.** Kuiter (1993: 391) figured two specimens as *Aseraggodes* sp., his upper figure labelled as the estuarine form, and the lower as coastal form. Upper figure (NMV A 25543–002, 82.5 mm SL) is included here as a paratype. When fresh, it was orangish brown with diffuse blackish blotches, the three along lateral line and one above the first blotch the largest; head and body with numerous, small, very irregular, dark-edged whitish spots; fin rays grey-brown with small dark-edged whitish spots, the ray tips white. The colour of the lower figure is very different, mottled lighter brown, likely to have been collected from a paler sand bottom.

This species was collected from sand in bays in NSW from depths of 4–10 m. It is among the most distinctive of the genus because of its angular and smoother scales and the profusion of fleshy cirri, in particular those on most of the lateral-line scales.

The covering of the ctenii of the scales by soft tissue except the small tips is also found in *A. normani*, but its scales have a rounded posterior margin instead of an angular one. It is easily distinguished from *lenisquamis* in other characters such as the branching of its lateral line on the ocular side of the head, its unbranched dorsal and anal rays, and the pelvic fins joined to the base of the genital papilla.

*Aseraggodes lenisquamis* is most similar to *A. nigrocirratus*, described below (see Remarks for the latter species).

The lower figure of this species in Kuiter (1993) mentioned above, was not identified initially as *A. lenisquamis* because of the broad interorbital space and the upper eye being almost directly over the interorbital space. However, the specimen was found as NMV A5827, 88 mm SL, from its shape, details of colour, and a distinct small tear in the caudal fin. The interorbital of the preserved specimen is much narrower, and the upper eye is more forward. A similar shrinkage of the interorbital with preservation was found in the holotype of *A. auroculus*.

*Aseraggodes magnoculus* sp. nov.

Figure 10, Tables 1–3, 8

**Holotype.** ROM 64830, 39.8 mm, New Caledonia, Isle Ua, E side, 22°42'40"S, 166°48'50"E, steep slope of fringing reef, with coral rock,

rubble, and sand at base, 9–18 m, rotenone, R. Winterbottom and P. Tirard, 13 Sep 1991.

**Paratypes.** ROM 76686, 29.2 mm, New Caledonia, just inside barrier reef (Recif Mbere) NW of Dumbéa Pass, 22°20'30"S, 166°14'5"E, large *Porites* coral head surrounded by sand, 3–6.5 m, rotenone, R. Winterbottom, G. Klassen and P. Tirard, 11 Sep 1991; BPBM 39691, 31.3 mm, same data as holotype.

**Diagnosis.** Dorsal rays 67–72; anal rays 51–53; dorsal rays branched except anterior 16–24 rays; anal rays branched; lateral-line scales 71–76, including 7–8 anterior to a vertical at upper end of gill opening; vertebrae 36; dorsal pterygiophores anterior to fourth neural spine 10; body depth 2.45–2.5 in SL; HL 4.15–4.3 in SL; eye diameter 3.95–4.2 in HL; upper eye overlapping about anterior one-third to one-half of lower eye; interorbital space narrow, the vertical distance separating eyes about one-third to one-sixth eye diameter; no caudal peduncle; very fine cirri on ventral edge of head; lateral line aligned with ventral edge of upper eye; longest dorsal ray 1.4–1.45 in HL; caudal fin rounded, its length 3.9–3.95 in SL; pelvic fins

Table 8. Proportional measurements of type specimens of *Aseraggodes magnoculus* as percentages of standard length

	Holotype	Paratype	Paratype
	ROM 64830	ROM 76686	B P B M 39691
Standard Length (mm)	39.8	29.2	31.3
Body depth	40.9	39.7	40.2
Body width	7.9	7.8	7.6
Head length	23.2	24.0	24.1
Snout length	8.9	9.3	9.2
Preorbital length	7.7	7.5	8.8
Eye diameter	5.5	5.8	6.1
Interorbital width	1.0	1.0	1.9
Upper-jaw length	7.5	7.5	7.4
Caudal-base depth	13.8	14.3	13.3
Predorsal length	6.3	6.2	6.1
Preanal length	26.6	27.5	26.9
Prepelvic length	20.6	21.0	21.8
First dorsal ray	7.3	7.5	7.0
Longest dorsal ray	16.8	16.6	17.2
First anal ray	8.8	8.7	8.9
Longest anal ray	15.8	15.8	16.6
Caudal-fin length	25.2	25.7	broken
Pelvic-fin length	12.8	12.6	12.6



Figure 10. Holotype of *Aseraggodes magnoculus*, ROM 64830, 39.8 mm, New Caledonia.



1.8–2.0 in HL, the tip of longest ray reaching base of second or third anal ray; colour of ocular side in alcohol light yellowish brown with 3 rows of dark brown blotches, one row below base of dorsal fin, one above base of anal and pelvic fins, and one with two largest blotches well-spaced on lateral line; other brown markings mainly vertically elongate, some enclosing small irregular areas of ground colour; fins pale yellowish except for faint dark blotches along base.

**Description.** Dorsal rays 72 (67–70); anal rays 53 (51–52); dorsal rays branched except first 16 (first 23–24 of paratypes); anal rays branched; caudal rays 18, the middle 16 branched, but not double-branched; pelvic rays 5, branched; rays of fins slender, the branches not broadly separated; lateral-line scales 71 (72–76), including 7–8 anterior to a vertical at upper end of gill opening; scales above lateral line on ocular side to dorsal-fin base 21–22; scales below lateral line to anal-fin base 23–24; vertebrae 36; erisma (counted as the first dorsal pterygiophore) about twice as thick as remaining pterygiophores, its inner half narrowly branched; next pterygiophore before tip of second neural spine; space between second and third neural spines with 5 pterygiophores; space between third and fourth neural spines with 3 pterygiophores (total of 10 dorsal pterygiophores anterior to fourth neural spine); ventroanterior margin of urohyal strongly curved, the two limbs, if projected, forming an angle of about 60°.

Body depth 2.45 (2.5) in SL; body width (thickness) 5.2 (5.1–5.3) in body depth; ventral profile of head posterior to mouth very slightly convex; HL 4.3 (4.15) in SL; snout length 2.6 in HL; eyes large, 4.2 (3.95–4.15) in HL; interorbital space very narrow, the least vertical interorbital width 23.2 (12.7–24.0) in HL; upper eye overlapping anterior one-fourth to one-third of lower eye; upper end of gill opening on a horizontal passing slightly ventral to lower eye; no caudal peduncle (base of last anal ray posterior to base of lowermost caudal ray); depth of body at base of caudal fin 1.7 (1.7–1.8) in HL.

Snout slightly overhanging lower jaw; maxilla nearly reaching to below center of eye, the upper jaw length (blind side) 3.1 (3.2–3.25) in HL; blind side of upper and lower jaws with a dense band of villiform teeth, obscured laterally because of a labial fold; no teeth on ocular side of jaws; tapering tubular anterior nostril of ocular side membranous, before upper edge of eye just above upper lip, nearly reaching anterior edge of pupil when laid back, its length equal to eye diameter; posterior nostril a slit in labial groove in front of lower eye; anterior nostril of blind side a slender tube only about twice as long as surrounding papillae, just above middle of upper lip; posterior nostril of blind side an opening covered by a triangular papilla-like structure, dorsoposterior to anterior nostril; internarial distance nearly equal to eye diameter.

Scales ctenoid on both sides (except partially embedded scales of lateral line); scales of ocular side of body with up to 10 cteni; only 1 or 2 rows of scales in interorbital space, with about another 5 rows extending onto medial and anterior part of each eye; scales on ocular side of head smaller anteriorly, replaced on snout by longitudinal rows of small fleshy papillae; scales on blind side of head anterior to a transverse demarcation just posterior to end of jaws replaced by a dense zone of fleshy papillae, largest above posterior half of upper lip; only fine cirri at front edge of snout and along ventral part of head. Lateral line straight midlaterally on both sides, projecting on ocular side toward middle of upper eye; lateral line of blind side altering to a row of sensory papillae on head (separated from surrounding papillae by a narrow papilla-free zone on ventral side that curves on head to tip of snout; supratemporal branch of lateral line on blind side of head clearly visible as a similar row of low sensory papillae just below basal sheath of scales on dorsal fin, less obvious on body posterior to head).

Dorsal and anal rays each with a lengthwise thin membranous ridge,

narrowing distally, less developed posteriorly; membranous ridges without cirri; small scales basally on ocular side of dorsal fin before about 15th ray, progressively fewer scales approaching 15th ray; anterior part of dorsal fin on blind side with small papillae, progressively fewer posteriorly, and absent after about the 24th ray.

Origin of dorsal fin anterior to upper eye, the predorsal length 3.7 (3.9–3.95) in HL; first dorsal ray (tip not free; tips of next few rays visible) 3.8 (3.7–3.95) in HL; longest dorsal ray 1.45 (1.4) in HL; origin of anal fin below base of seventeenth dorsal ray, slightly posterior to end of opercular membrane, the preanal length 3.75 (3.65–3.7) in SL; length of first anal ray 3.75 (3.65) in HL; longest anal ray 1.45 (1.45–1.5) in HL; caudal fin rounded, 3.95 (3.9) in SL; pelvic fins adjacent on ventral edge of body, third and fourth pelvic rays longest, reaching to base of third anal rays, 1.8 (1.9) in HL; anus anterior to first anal ray; genital papilla short, dorsoposterior to anus, and not connected by membrane to ocular-side pelvic fin.

Colour of holotype in alcohol: ocular side light yellowish brown with 3 rows of dark brown blotches, one below base of dorsal fin, one above base of anal and pelvic fins, and one midlateral, the two largest blotches well-spaced on lateral line; other lighter brown markings irregular, mainly transversely elongate, some enclosing small areas of lighter ground colour; fins pale yellowish except for faint dark blotches along base; blind side uniform pale yellowish.

**Etymology.** This species is named *magnoculus* from the Latin *magnus* for large and *oculus* for eye, in reference to its having the largest eyes, relative to the head length, of any species of the genus examined.

**Remarks.** *Aseraggodes magnoculus* is described from three small specimens collected in two stations from sand and rubble in coral-reef areas of New Caledonia within the depth range of 3–18 m. No gonad was detected in the largest specimen, so it may be immature. *Aseraggodes auroculus*, described above, appears to be the most similar species to *A. magnoculus*. The two share the same body depth, large eyes, and number of vertebrae, dorsal pterygiophores anterior to the fourth neural spine, dorsal rays, and lateral-line scales. *A. auroculus* differs in having a higher count of anal rays (56 or 57, compared to 51–53 for *magnoculus*), a larger head (hence the eye size relative to the head is smaller than that of *magnoculus*), and in having shorter fins.

#### *Aseraggodes melanostictus* (Peters, 1877)

Figure 11, Tables 1–3

*Solea melanosticta* Peters, 1877: 845

*Aseraggodes melanostictus*.—Randall and Bartsch, 2005: figs. 3–5

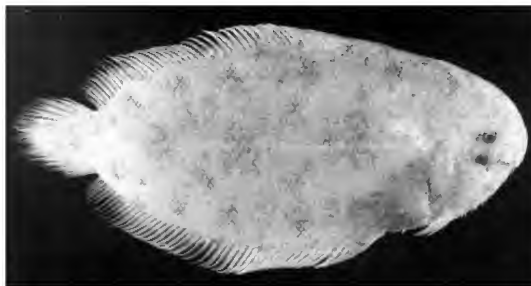


Figure 11. *Aseraggodes melanostictus*, AMS I.24499–003, 86.5 mm, North Reef, Great Barrier Reef.

(of holotype).

*Type locality.* Bougainville

*Diagnosis.* Dorsal rays 74–75, unbranched; anal rays 53–54, unbranched; caudal rays 18 (uppermost and lowermost 2 rays simple, middle 12 double-branched); pelvic rays 5, unbranched; lateral-line scales on ocular side 78–79, including 9 anterior to a vertical at upper end of gill opening; scales of ocular side of body with 12–16 cteni; scales anteriorly on head progressively shorter, with fewer cteni, modified to small flattened papillae, each with a small flat brown cirrus in zone anteriorly on snout; no broad lappet-like cirri at front of snout or on ventral edge of head, instead cylindrical cirri of variable size, the longest less than pupil diameter; well-spaced slender cirri on opercular edge of gill opening on both sides; vertebrae 38; dorsal pterygiophores anterior to fourth neural spine 11–13; body depth 2.3–2.35 in SL; HL 4.35–4.5 in SL; snout slightly overhanging lower lip when mouth closed; lateral line directed anteriorly toward dorsal edge of upper eye; eye diameter 6.4–6.8 in HL; upper eye overlapping anterior one-half to three-fourths of lower eye; least vertical interorbital space 8.3–8.6 in HL; upper end of gill opening at level of ventral edge of lower eye; no caudal-peduncle; depth at base of caudal fin 1.5–1.65 in HL; longest dorsal ray 1.45 in HL; caudal fin rounded, 5.1–5.8 in SL; ocular-side pelvic fin on ventral edge of body, its base slightly anterior to that of fin of blind side; third pelvic ray longest, 2.0–2.8 in HL, the tip reaching base of second anal ray; lengthwise membranous ridge on dorsal rays of both sides, progressively reduced posteriorly; small scales on about basal half of membranous ridge of anterior dorsal rays of ocular side; edge of membranous ridge of about first 15 blind-side dorsal rays with prominent cirri; colour of ocular side in alcohol light brown, the scale edges darker than centers,

with faint irregular dark-edged pale markings over head and body, and very irregular dark brown blotches, most much larger than eye, the two largest on lateral line to either side of middle of body; fins with dark dots. Largest of two known specimens, 86.5 mm SL.

*Remarks.* Randall and Bartsch (2005) described a specimen from Kwajalein Atoll, Marshall Islands identified as *Aseraggodes melanostictus* by Woods in Schultz and collaborators (1966) from Kwajalein Atoll, Marshall Islands as a new species, *A. heraldi*. They illustrated an x-ray and two photographs of the holotype of *melanostictus* from the Museum für Naturkunde in Berlin (ZMB 9814, 74 mm SL) and listed differences from *A. heraldi*, notably its having unbranched dorsal and anal rays.

The holotype of *A. melanostictus* was collected in 73 m off the island of Bougainville. A second specimen, AMS I.24499-003, 86.5 mm, sent on loan from the Australian Museum, is provisionally identified as this species. It was dredged in 115 m NE of North Reef of the Great Barrier Reef (23°8'S, 152°12'E) by W. Ponder et al. on 14 Dec 1977. It differs in having 13 instead of 11 dorsal pterygiophores anterior to the fourth neural spine, and in some proportional measurements, but none clearly beyond expected infraspecific variation.

#### *Aseraggodes nigrocirratus* sp. nov.

Figure 12, Tables 1–3, 9

*Holotype.* AMS I.26535-001, female, 79.0 mm, Australia, NSW, SE of Evans Head, off Iluka, 29°20'S, 153°29'E, 40–51 m, trawl, FRV “Kapala”, 24 May 1986.

*Paratypes.* AMS I.321, 89.4 mm, Australia, NSW, Sydney, Port Jackson, 33°51'S, 151°16'E, 1886; AMS I.636, mature female, 68.8 mm SL, Australia, NSW, Sydney, Port Jackson, 33°51'S, 151°16'E, J.

Table 9. Proportional measurements of type specimens of *Aseraggodes nigrocirratus* as percentages of standard length

	Holotype		Paratypes			
	AMS I.26535	BPBM 39610	AMS IA.5449	AMS IA.5449	AMS I.636	AMS I.321
Standard Length (mm)	79.0	52.3	55.0	56.8	68.8	89.4
Body depth	41.0	38.2	39.7	40.7	42.5	42.7
Body width	8.1	7.6	7.1	7.2	7.6	7.7
Head length	21.7	21.0	21.4	21.3	20.8	21.3
Snout length	7.4	7.5	7.2	7.3	7.3	7.2
Preorbital length	6.2	6.1	5.9	6.0	5.9	5.8
Eye diameter	3.7	4.0	3.8	3.7	3.7	3.4
Interorbital width	2.0	1.9	2.1	2.1	2.2	2.2
Upper-jaw length	6.3	6.0	6.4	6.3	6.1	6.4
Caudal-base depth	13.9	12.8	13.2	14.1	14.7	14.6
Predorsal length	5.7	6.1	5.7	5.8	5.7	5.6
Preanal length	26.6	25.7	26.5	26.8	24.8	25.6
Prepelvic length	19.2	20.3	19.8	19.3	19.9	19.4
First dorsal ray	7.8	7.1	7.5	8.1	8.0	7.6
Longest dorsal ray	12.7	13.3	13.5	13.2	13.2	12.0
First anal ray	7.7	7.9	8.0	8.5	7.8	7.3
Longest anal ray	12.6	13.3	13.7	13.1	13.2	12.1
Caudal-fin length	21.4	23.0	23.2	broken	23.1	20.8
Pelvic-fin length	10.7	11.2	11.6	11.4	10.9	10.5

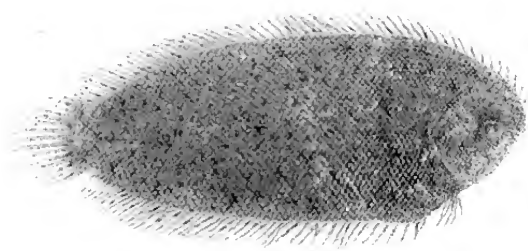


Figure 12. Holotype of *Aseraggodes nigrocirratus*, AMS 1.26535-001, 79.0 mm SL, off Iluka, NSW (K.J. Graham).

Hunt, 1886; AMS 1A.5449, 2: 55.0–56.8 mm, NSW, Pittwater, 33°38'S, 151°18'E, dredge, M. Ward, 1932; NMV A 21382, 61 mm, Sydney, Coogee Beach, 33°55'S, 151°15'E, R.H. Kuiter, 26 Jan 1980; AMS 1.26535-008, 2: 65.5–82 mm, and ROM 77681, 67 mm, same data as holotype.

**Diagnosis.** Dorsal rays 63–68; anal rays 47–53; most dorsal and anal rays branched; lateral-line scales 61–67, including 8–9 anterior to a vertical at upper end of gill opening; one to three pores beneath some scales on ocular side of body near base of dorsal and anal fins; vertebrae 36–38; dorsal pterygiophores anterior to fourth neural spine 8–9; body depth 2.35–2.65 in SL; head short, length 4.7–4.85 in SL; upper lip not overlapping lower lip when mouth closed; no prominent cirri on ventral edge of head; lateral line aligned with dorsal third of upper eye; eye diameter 4.6–6.25 in HL; upper eye overlapping anterior half to two-thirds of lower eye; interorbital space narrow, the vertical distance separating eyes about half eye diameter; no caudal peduncle; longest dorsal ray 1.5–1.75 in HL; caudal fin slightly pointed, its length 3.95–4.8 in SL; pelvic fins 1.8–2.0 in HL, the tip of longest ray reaching base of third anal ray; ocular side light brown with numerous small variable dark brown spots of variable size, some in form of a small cross; cirri on lengthwise membranous ridge of rays of dorsal and anal fins dark brown (appearing as small dark spots without magnification).

**Description.** Dorsal rays 64 (63–68); anal rays 49 (47–53); dorsal and anal rays unbranched (none double-branched), except unbranched first 9 dorsal and anal rays (first 19 dorsal and anal rays and last few rays of 43.6-mm paratype); caudal rays 18, branched, middle 16 double-branched; pelvic rays 5, branched; lateral-line scales on ocular side 65 (61–67), including 8–9 anterior to a vertical at upper end of gill opening; 1 scale above lateral line to dorsal-fin base on ocular side about 20; scales below lateral line to anal-fin base about 24 (23–24); vertebrae 37 (two paratypes with 36, five with 37, and two with 38); erisma (counted as the first dorsal pterygiophore) about twice as thick as remaining pterygiophores, its inner two-thirds branched; only erisma before the second neural spine; space between second and third neural spines with 5 pterygiophores; space between third and fourth neural spines with 3 (2–3) pterygiophores, total 9 (8–9) dorsal pterygiophores anterior to fourth neural spine; ventroanterior margin of urohyal forming an angle of about 80° (65–80°), the corner slightly rounded.

Body depth 2.45 (2.35–2.65) in SL; body width 5.05 (5.05–5.85) in body depth; dorsal profile of head slightly more convex than ventral; HL 4.6 (4.7–4.85) in SL; snout length 2.95 (2.7–3.0) in HL; preorbital length 3.5 (3.3–3.75) in HL; eye diameter 5.85 (4.6–6.25) in HL; least vertical interorbital width 10.8 (8.9–11.1) in HL; upper eye over-

lapping anterior one-half to four-fifths of lower eye; upper end of gill opening on a level one-half to one eye diameter below ventral edge of lower eye; no caudal peduncle (base of lowermost caudal ray above or slightly anterior to base of last anal ray); depth of body at base of caudal fin 1.55 (1.4–1.75) in HL.

Front of upper lip not overlapping lower lip when mouth closed; maxilla extending slightly posterior to a vertical at front edge of lower eye, the upper jaw length (measured on blind side) 3.45 (3.3–3.6) in HL; blind side of upper and lower jaws with a dense band (broader posteriorly) of slender, inward-projecting, slightly curved teeth, up to about 7 rows in lower jaw and 5 or 6 in upper jaw (teeth on upper jaw beneath a thin labial fold, hence difficult to see); anterior nostril a tapering membranous tube anterior to upper edge of lower eye, just reaching fleshy base of orbit when laid back (reaching to edge of eyeball in smaller paratypes), its length in holotype about three-fourths eye diameter; posterior nostril an oblique slit in labial groove in front of base of lower eye; anterior nostril of blind side a slender membranous tube just above anterior third of upper lip; posterior nostril of blind side a short strongly tapering membranous tube dorsoposterior to anterior nostril; internarial distance on blind side about three-fourths eye diameter.

Scales ctenoid on both sides (cycloid on lateral line and partially embedded); scales of ocular side of body usually with 8–10 cteni (up to 12 in largest paratype); one to three pores beneath some scales on ocular side of body near base of dorsal and anal fins; 3 rows of scales in interorbital space, with about another 3 rows extending onto medial and anterior part of each eye; scales on ocular side of head progressively smaller anteriorly and ventrally, the most anterior at front of snout very small and without cteni; fleshy front of snout with small short cirri on edge; scales on blind side of head gradually replaced anteriorly by papillae, ending with small slender papillae on edge of snout; broad zone of small fleshy papillae on blind side dorsal to upper jaw; ventral edge of head with cirri as long as half eye diameter; no cirri along edge of operculum at gill opening on either side. Lateral line straight midlaterally on both sides of body, directed on ocular side toward dorsal third of upper eye; supratemporal branch of lateral line on blind side of head faintly visible, continuing dorsally 2 to 3 scale rows below dorsal fin, persisting to about middle of body.

Dorsal and anal fins with a basal sheath of 2 to 3 rows of scales; lengthwise thin membranous ridge basally on dorsal and anal rays with well-spaced dark brown cirri on free edges except posterior rays; small scales basally on membranous ridges of anterior dorsal rays on both sides (first 19 rays of holotype), the height of the scale bands progressively shorter posteriorly; about basal third of caudal fin with scales on both sides, with small, well-spaced, isolated scales, with a few prominent cteni on each side of rays to within outer third of fin.

Origin of dorsal fin anterior to lower fourth of upper eye, the predorsal length 3.8 (3.25–3.8) in HL; first dorsal ray 2.8 (2.6–2.95) in HL; longest dorsal ray 1.7 (1.5–1.75) in HL; origin of anal fin below base of fifteenth or sixteenth dorsal ray and about one-half eye diameter behind posterior end of operculum, the preanal length 3.8 (3.75–4.15) in SL; length of first anal ray 2.8 (2.5–2.9) in HL; longest anal ray 1.7 (1.5–1.75) in HL; caudal fin slightly pointed, relatively shorter with growth, 4.7 (3.95–4.8) in SL; ocular-side pelvic fin on ventral edge of body; base of blind-side fin adjacent anteriorly, its origin slightly posterior to ocular-side fin; third pelvic ray of each fin longest, reaching to base of third anal ray, 2.0 (1.8–2.0) in HL; anus directly before base of first anal ray at end of short semicircular column of ridged fleshy tissue, an upper anterior triangular part covering opening; genital papilla on ocular side of base of first anal ray, very large, its length equal to orbit diameter; membrane from near base of last pelvic ray of ocular side joined to extreme base of genital papilla.

Colour of holotype in alcohol: ocular side light grey-brown with numerous small dark brown spots on head, body, and basal scaly part



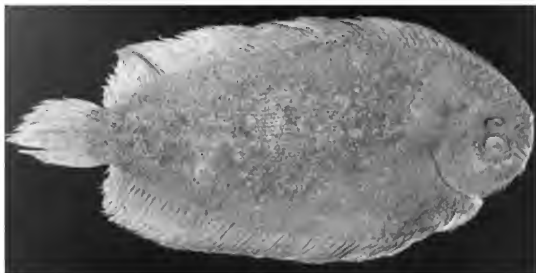


Figure 13. Holotype of *Aseraggodes normani*, BMNH 1925.7.22.73, 109 mm SL, Queensland.

of caudal fin, some as small dark crosses from dark edges of adjacent scales; dorsal and anal fins with translucent membranes, the rays light yellowish brown, most with 1–3 small dark brown spots associated with a fleshy cirrus; naked part of caudal fin like dorsal and anal fins, but small dark spots on the rays without a cirrus; blind side of body pale yellowish, slightly dusky in a broad peripheral zone. Figure 12 taken of a fresh specimen, very similar to colour in preservative; pale spots on figure from missing scales.

**Etymology.** Named *nigrocirratus* from the Latin, in reference to the black cirri on the dorsal and anal rays of the ocular side of this species.

**Remarks.** *Aseraggodes nigrocirratus* is presently known only from NSW from latitudes 29°20'S to 33°55'S, from inshore to about 50 m.

Randall and Meléndez (1987) mentioned this species in their description of *Aseraggodes bahamondei* as probably undescribed, noting that it also has pores under some scales of the ocular side near the base of the dorsal and anal fins. They attributed the presence of these pores in *bahamondei* to the production of a strong skin toxin, probably comparable to that of the species of *Pardachirus* (Clark and George, 1979).

Although *Aseraggodes bahamondei* is similar in its colouration, general morphology, and the low number of dorsal pterygiophores anterior to the fourth neural spine to *A. nigrocirratus*, it is readily distinguished by having a caudal peduncle (though this difference is actually very slight), 39 to 40 vertebrae, 75–86 lateral-line scales, and by attaining a significantly larger maximum size of at least 156 mm SL.

Of the known species of the genus, *A. nigrocirratus* is most similar to *A. lenisquamis*, described above. The two have the same vertebral count (36–38), the same number of dorsal pterygiophores anterior to the fourth neural spine (8–9), and nearly the same number of dorsal and anal rays and lateral-line scales (see Tables 1–3). They differ mainly in the structure of the scales. Those of *nigrocirratus* are typical of most species of the genus, with prominent cteni that project well beyond the posterior margin of the scales, and the exposed surface of the scales with a pattern like miniature scales. The scales of *lenisquamis* are generally more pointed posteriorly and are covered with soft cutaneous tissue, such that only the tips of the cteni project beyond the scale margins (each capped with soft tissue). Also the lateral-line scales and scattered other scales of *lenisquamis* have small fleshy cirri. Three different propor-

tional measurements of the two species are evident in Tables 7 and 9. *A. lenisquamis* has a longer snout, broader caudal-fin base, and is broader, and shorter caudal fin.

Six specimens of AMS I.24035-003, 42.0–52.3 mm SL, collected in 1 m at Wagstaff Point, Brisbane Waters, NSW, 33°28'S, 151°21'W, in 1982 include four provisionally identified as *A. nigrocirratus* and two of about 45 mm SL that appear to be hybrids of *A. lenisquamis* and *A. nigrocirratus*. The latter two specimens have scales of both types, though mainly those typical of *A. lenisquamis*, and only a few short cirri on lateral-line scales near the middle of the body. Both specimens are misshapen and difficult to measure. The four specimens identified as *A. nigrocirratus* are excluded from the type series.

Similarly, the two specimens of AMS I.38279-001, 79.4–83.0 mm, collected by trawl in 48 m off the Clarence River, NSW at 29°19.5'S, 153°24'E, include one of *A. lenisquamis* (the larger) and one that is regarded as a hybrid of *A. nigrocirratus* and *A. lenisquamis*. This lot is also undivided, and the specimen of *lenisquamis* is not designated as a paratype. The presumed hybrid has scales characteristic of each of the species, and it is intermediate in the three proportional measurements that are diagnostic.

#### *Aseraggodes normani* Chabanaud

Figure 13, Tables 1–3

*Aseraggodes melanostictus*.—Norman, 1926: 290, fig. 12 (off Gladstone, Queensland) (non Peters)

*Aseraggodes normani* Chabanaud, 1930: 241.

**Material examined.** Queensland: BMNH 1925.7.22.73, 109 mm, holotype of *Aseraggodes normani*. WSW of Townsend Island, 22°21.5'S, 150°25'E, AMS I.34377-005, 83 mm. 2 km NE of Cape Clinton, 22°32'S, 150°48'E, AMS I.34399-032, 93.5 mm. 2 km NE of Cliff Point, 22°35'S, 150°49'E, AMS I.34361-024, 3: 74.5–89 mm. Off Gladstone, AMS IA.2993, 104.5 mm. Off Bustard Head, 24°1'S, 151°46'E, AMS IB.1105, 97.5 mm. Moreton Bay, AMS I.484, 116 mm.

**Type locality.** Coast of Queensland.

**Diagnosis.** Dorsal rays 64–71, anal rays 50–52; dorsal and anal rays unbranched (Chabanaud incorrect in reporting bifid tips); pelvic rays 5; caudal rays 18, 14 branched; lateral-line scales 68–73 (counted to origin of dorsoanterior branch on head); only tips of cteni projecting beyond posterior edge of scales, with at most 8 cteni tips posteriorly on body, fewer anteriorly); eyes separated by 3 rows of scales at narrowest place, with an additional row medially and anteriorly on each eye; vertebrae 35–36 (usually 35); dorsal pterygiophores anterior to fourth neural spine 10–11; body depth 2.3–2.55 in SL; HL 4.4–4.8 in SL; snout length 2.3–2.5 in HL; scales anteriorly on head replaced by slender cirri, progressively longer, those at ventral edge of head and front of snout up to three-fourths eye diameter in length; lateral line aligned with dorsal edge of upper eye, ending with a dorsoanterior branch of 7–9 pored scales, straight branch of 4–6 scales, and ventral branch of 7–9 scales; no pores detected beneath scales on ocular side of body; eye diameter 5.0–6.5 in HL; upper eye overlapping anterior one-half to three-fourths of lower eye; narrowest vertical interorbital space 8.2–9.0 in HL; upper end of gill opening at level of

ventral fleshy edge of lower eye; tubular anterior nostril broad, not reaching fleshy base of lower eye when laid back; no caudal peduncle; depth at base of caudal fin 1.55–1.8 in HL; caudal fin rounded, its length 4.1–4.5 in SL; longest dorsal ray 1.35–1.5 in HL; blind side of dorsal and anal rays with a lengthwise thin membranous ridge, broad at base and narrowing as it extends up to three-fourths ray length anteriorly, progressively shorter and narrower posteriorly; edge of membrane on anterior rays of blind side of dorsal fin with cirri; pelvic fins 1.9–2.05 in HL, the tip of longest ray extending to base of second or third anal ray; ocular-side pelvic fin distinctly anterior and larger than fin of blind side; both fins broadly joined by membrane from their fifth rays and jointly to the large genital papilla about one-half length above its base; colour in alcohol light brown, densely dotted with black and short black scale edges; scattered roundish pale spots smaller than eye variously present, some free of black dots; median fins with black dots, but fewer than on body; one specimen with a few large dark blotches on lateral line and on either side of lateral line. Largest specimen examined, 116 mm SL.

**Remarks.** Known only from off the coast of Queensland from 22.5° to 27° S, taken by trawls at depths of 15 to 27 m. Norman (1926) reported three specimens, 130–142 mm total length, collected off Queensland during the experimental cruises of R/V “Endeavour”, 1909–1914, as *Aseraggodes melanostictus* Peters, previously known from a single specimen taken in 73 m off New Britain. Chabanaud (1930a) found one of Norman’s three specimens at the Natural History Museum, London (BMNH). Recognizing it as misidentified, he named it in honour of J.R. Norman. An additional (non-type) “Endeavour” specimen in the Australian Museum was collected off Gladstone, 23°S 151°E on 9 Jul 1910.

Chabanaud (1943) established the valid genus *Synclidopus* for the species *Solea macleayanus*, but he erred in placing *Aseraggodes normani* as a second species of this genus.

#### *Aseraggodes pelvius* sp. nov.

Figure 14, Tables 1–3, 10

**Holotype.** AMS IB.6134, 67.5 mm, Australia, Queensland, Great Barrier Reef, Swain Reefs, Gilette Cay, rotenone, Australian Museum Expedition, October 1962.

**Diagnosis.** Dorsal rays 71; anal rays 49; lateral-line scales 81; vertebrae 36; dorsal pterygiophores anterior to fourth neural spine 14; body depth 2.45 in SL; HL 4.75 in SL; eye diameter 6.4 in HL; upper eye overlapping anterior half of lower eye; interorbital space narrow, 12.0 in HL; caudal peduncle present, its depth 1.45 in HL, its length 10.0 in HL; prominent lappet-like cirri on front of snout and ventral edge of head; lateral line aligned with dorsal edge of upper eye; longest dorsal ray 1.25 in HL; membranous edges of anterior dorsal rays with a row of tubercle-like papillae, many with cirri, a few darkly pigmented; caudal fin rounded and moderately long, 3.4 in SL; pelvic fins long, 1.6 in HL, the tip of longest ray reaching base of fifth anal ray; colour of ocular side in alcohol pale yellowish brown with numerous irregular pale spots, none as large as eye, and many smaller brown blotches and dots, the most conspicuous along

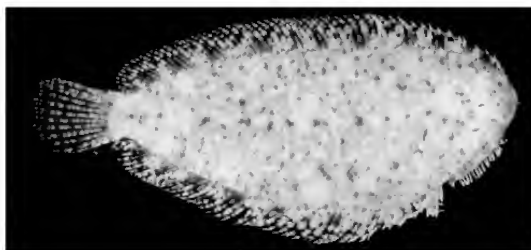


Figure 14. Holotype of *Aseraggodes pelvius*, AMS IB.6134, 67.5 mm, Swains Reefs, Great Barrier Reef.

Table 10. Proportional measurements of holotype of *Aseraggodes pelvius* as percentages of standard length

Standard Length (mm)	67.5
Body depth	41.2
Body width	7.8
Head length	21.0
Snout length	7.6
Preorbital length	8.1
Eye diameter	3.3
Interorbital width	2.1
Upper-jaw length	6.7
Caudal-peduncle depth	14.2
Caudal-peduncle length	1.7
Predorsal length	6.5
Preal length	25.2
Prepelvic length	20.3
First dorsal ray	7.5
Longest dorsal ray	16.5
First anal ray	10.3
Longest anal ray	16.6
Caudal-fin length	29.5
Pelvic-fin length	10.2

middle of lateral line.

**Description.** Dorsal rays 71, branched except first 9, the tips broadly free; anal rays 49, branched except first; caudal rays 18, the uppermost and lowermost unbranched, the middle 14 double-branched; pelvic rays 5, branched except last ray of blind side; lateral-line scales 81, including 11 anterior to a vertical at upper end of gill opening; scales on ocular side above lateral line to dorsal-fin base 27; scales below lateral line to anal-fin base about 33; vertebrae 37; erisma (counted as the first dorsal pterygiophore) about twice as thick as remaining pterygiophores, its inner three-fourths narrowly branched; next 2 pterygiophores before tip of second neural spine; space between second and third neural spines with 7 pterygiophores; space between third and fourth neural spines with 3 pterygiophores (total of 13 dorsal pterygiophores anterior to fourth neural spine); ventro-anterior margin of urohyal forming an angle of about 80°, the corner slightly rounded.

Body depth 2.45 in SL; body width 5.3 in body depth; HL 4.75 in SL; ventral profile of head below mouth nearly straight; eye diameter 6.4 in HL; least vertical interorbital width 10.0 in HL; a vertical at posterior edge of upper eye (edge of dark eyeball) passing through middle of lower eye; ventral edge of lower eye one-half eye diameter above level of upper end of gill opening; caudal-peduncle depth 1.45 in HL; caudal-peduncle length 10.0 in HL.

Snout not overhanging lower lip when mouth closed; maxilla extending to below middle of lower eye, the upper jaw length (blind side) 3.15 in HL; jaws too firmly closed to obtain details of dentition; anterior nostril a tapering membranous tube anterior to upper edge of lower eye, reaching anterior edge of eye ball when laid back, its length equal to eye diameter; posterior nostril an oblique slit in labial groove directly in front of ventral third of lower eye; anterior nostril of blind side a very slender membranous tube nearly an eye diameter in length just above anterior third of upper lip; posterior nostril of blind side an eye diameter dorsoposterior to anterior nostril, covered by a broadly curved pointed flap on ventral side.

Scales ctenoid on both sides (except those of lateral line, partially embedded); scales of ocular side with 11–14 cteni; 3 rows of scales in interorbital space, with about another 4 or 5 rows extending onto medial and anterior part of each eye; scales on both sides of head progressively smaller anteriorly and ventrally, with fewer cteni, replaced more anteriorly with isolated papillae and at front of snout by cirri; 15 large lappet-like cirri along ventral edge of head below mouth, and several at front of snout; slender well-spaced cirri along edge of opercle at the gill opening on both sides. Lateral line straight mid-laterally on both sides, directed on ocular side toward dorsal edge of upper eye; supratemporal branch of lateral line curving at front of head on blind side, continuing posteriorly onto body 2 to 3 scale rows below dorsal fin, becoming obscure posterior to base of about 23rd dorsal ray.

Dorsal and anal fins with a basal sheath of 2 to 3 rows of scales; a thin membranous lengthwise ridge on dorsal and anal rays of both sides, progressively smaller posteriorly; front of dorsal fin on ocular side densely covered with papillae to base of about fourth ray; edge of membranous ridge on rays of about anterior third of dorsal fin with a row of small tubercle-like papillae, most ending in a slender cirrus; rows of similar papillae on anterior dorsal rays of blind side, but without cirri; small scales extending out on anterior dorsal rays, progressively reduced posteriorly, and absent beyond 25th dorsal ray; small tubercle-like papillae on basal part of rays of anal fin on ocular side, disappearing posterior to 20th ray.

Origin of dorsal fin anterior to lower edge of upper eye, the pre-dorsal length 3.25 in HL; first dorsal ray 2.8 in HL; first 5 dorsal rays free of membrane at tips; longest dorsal ray 1.25 in HL; origin of anal fin below base of 22nd dorsal ray and slightly behind posterior end of opercular membrane, the preanal length 4.0 in SL; length of first anal ray 2.05 in HL; longest anal ray 1.25 in HL; caudal fin rounded and moderately long, 3.4 in SL; pelvic fins adjacent on ventral edge of body; ocular-side pelvic fin slightly longer, the second and third pelvic rays longest, reaching to base of fifth anal ray, 2.05 in HL; anus anterior to first anal ray; genital papilla on ocular side of anus, about equal in length to pupil diameter.

Colour of ocular side in alcohol pale yellowish brown with numerous irregular pale spots (probably near-white in life), some approaching eye size; many brown blotches and brown dots (mainly from dark posterior edge of scales) scattered on head and body, the middle three or four of about ten along lateral line the most conspicuous (each covering 4 or 5 lateral-line scales); dorsal, anal, and pelvic fins with pale yellowish rays and translucent membranes; a few isolated cirri of dorsal fin brown; scaled basal part of caudal fin coloured like body, the rest of fin with pale yellowish rays and transparent membranes, except for small scales on rays that are brown; blind side of body pale yellowish brown with no markings.

**Etymology.** Named *pelvicus* from the Latin *pelvis*, in reference to the long pelvic fins, the longest for species of the genus.

**Remarks.** This species is known only from the holotype from the Swain Reefs of the Great Barrier Reef of Australia. It

appears to be most closely related to *Aseraggodes ramsaii* from Lord Howe Island and New Caledonia and to *A. whitakeri*, wide-ranging in islands of the Pacific. It shares the same counts of vertebrae, dorsal pterygiophores, dorsal rays, and anal rays with these two species. It differs from both in its smaller head, smaller eye, and longer dorsal and pelvic fins. *Aseraggodes ramsaii* has a higher number of lateral-line scales, 86–88, compared to 81 for *pelvicus*, but additional specimens are needed to confirm this difference. The series of small tubercle-like papillae at the edge of the membranous ridges of the dorsal and anal rays, many with a small cirrus, and the long pelvic fins appear to be unique to *A. pelvicus*.

### *Aseraggodes ramsaii* (Ogilby, 1889)

Figure 15, Tables 1–3

*Solea ramsaii* Ogilby, 1889: 70, pl. 3 fig. 4.

*Aseraggodes haackeanus ramsaii* — Munro, 1957: 73.

*Aseraggodes haackeanus*. — Hoesé in Allen et al., 1976: 437.

*Aseraggodes ramsaii*.—Randall and Meléndez, 1987: 105.

Material examined. Lord Howe Island: AMS I.1951, 57 mm, holotype of *Solea ramsaii*; AMS I.5387, 63.5 mm; BPBM 34265, 41.7 mm. New Caledonia: lagoon near SE end of St Vincent Pass (22°26'S, 165°57'48"E).

**Type locality.** Lord Howe Island.

**Diagnosis.** Dorsal rays 69–72, branched except first 14–22 rays; anal rays 47–50, all but branched; caudal rays 18 (uppermost and lowermost two rays simple, middle 12–14 double-branched); pelvic rays 5; lateral-line scales on ocular side 86–88, including 12 anterior to a vertical at upper end of gill opening; scales with 10–14 cteni; scales progressively shorter anteriorly on head and with fewer cteni; 2 rows of scales in narrowest interorbital space, with small scales in 4 or 5 rows extending onto median and anterior edges of eyes; broad lappet-like cirri on ventral margin of head; vertebrae 36; dorsal pterygiophores anterior to fourth neural spine 13–14 (14 in holotype); body depth 2.4–2.6 in SL; HL 4.45–4.5 in SL; upper lip slightly overhanging lower lip when mouth closed; eye diameter 4.05–4.65 in HL; posterior edge of upper eye over middle of lower eye; interorbital space narrow, the least vertical distance separating eyes 12.3–13.3 in HL; lateral line angling upward anteriorly, directed toward dorsal edge of upper eye; ventral edge of lower eye about one-half eye diameter



Figure 15. *Aseraggodes ramsaii*, BPBM 34265, 41.7 mm, New Caledonia.



above upper end of gill opening; caudal peduncle present, its length 8.1–10.8 in HL; longest dorsal ray 1.65–1.7 in HL; caudal fin rounded, 3.85–3.95 in SL; ocular-side pelvic fin on ventral edge of body and slightly anterior to fin of blind side, the second or third ray longest, 2.3–2.35 in HL, the tip reaching to base of second or third anal rays; small scales extending nearly to dorsal-fin margin anteriorly on both sides, the scale coverage gradually reduced to fifteenth to 20th ray, and absent posteriorly; a thin membranous lengthwise ridge basally on dorsal and anal rays, disappearing posteriorly; a dark brown cirrus occasional on membranous ridges of dorsal rays on ocular side. Colour of holotype in alcohol “pale yellow with many small black spots and short wavy lines on head and body, which on the lateral line take the form of streaks extending from two to five scales” (Ogilby, 1889). Largest of 3 specimens examined, 63.5 mm SL.

**Remarks.** Munro (1957) regarded *Aseraggodes ramsaii* as a subspecies of *A. haackeanus* (Steindachner). He was followed by Hoesle in Allen et al. (1976), who reported two specimens from Lord Howe Island collected from sand outside the lagoon in 5–25 m (specimens not found). Randall and Meléndez (1987) showed that *A. ramsaii* and *A. haackeanus* are readily separated by counts of dorsal rays, anal rays, and lateral-line scales. There is also a consistent difference in the number of dorsal pterygiophores before the fourth neural spine, 14–15 for *ramsaii* and 7–9 for *A. haackeanus*.

*Aseraggodes ramsaii* is otherwise known from the holotype in the Australian Museum, one other AMS specimen from Lord Howe Island, and one reported here from New Caledonia collected by Michel Kulbicki and the author in 2–4 m. The New Caledonia specimen was first believed to be *Aseraggodes holcomi* Randall, described from five specimens from the Hawaiian Islands. It was reidentified as *A. ramsaii* after comparison with the Lord Howe Island specimens. The two species are very similar, differing in *A. holcomi* having a broader interorbital space (6.8–10.9 in HL, compared to 12.2–13.2 for *ramsaii*), longer pelvic fins (1.85–2.1 in HL, compared to 2.3–2.35 for *ramsaii*), and a higher average count of lateral-line scales (87–96, compared to 86–88 for *ramsaii*).

#### *Aseraggodes whittakeri* Woods

Figures 16, 17, Tables 1–3

*Aseraggodes melanostictus*.—Schultz, 1943: 60 (Hull Island,

Phoenix Islands) (non *Aseraggodes melanostictus* Peters).

*Aseraggodes whittakeri* Woods in Schultz et al., 1966: 71, fig. 150.

*Aseraggodes* sp.—Wass, 1984: 31 (Taema Bank, Tutuila, American Samoa).

**Material examined.** Marshall Islands: Rongelap Atoll, USNM 141765, 38 mm (holotype). Caroline Islands: Kapingamarangi Atoll, CAS 205944, 28 mm. Coral Sea: Chesterfield Bank, BPBM 33731, 22 mm. New Caledonia, ROM 64828, 42 mm; ROM 64829, 37 mm; ROM 64831, 21.5 mm. Fiji: Ringgold Islands, BPBM 20863, 32 mm. American Samoa: Tutuila, Taema Bank, BPBM 24113, 43.0 mm; BPBM 24130, 2: 25–25.5 mm. Phoenix Islands: Hull Island, USNM 115223, 34 mm. Society Islands: Moorea, ROM 61360, 14 mm; ROM 61361, 23 mm.

**Type locality.** Rongelap Atoll, Marshall Islands.

**Diagnosis.** Dorsal rays 71–78; anal rays 48–53; pelvic rays 5 (3 in one side on one aberrant specimen); caudal rays 18, 14 branched (17 rays, 13 branched in one specimen); lateral-line scales 77–86, including 10–12 anterior to a vertical at upper end of gill opening; most scales of ocular side of body with 8–10 cteni (up to 11 on largest specimens); narrowest interorbital space with 2 scales; eyes with only 1 or 2 scales extending onto medial edge, and only about 3 rows anteriorly; vertebrae 36–38; dorsal pterygiophores anterior to fourth neural spine 14–15; body depth 2.55–2.75 in SL; HL 4.1–4.35 in SL; an overhanging fleshy snout, the lower edge of upper lip usually extending ventral to lower lip and jutting anterior to profile of head below mouth (more evident in smaller specimens); eye diameter 4.7–5.55 in HL; upper eye varying from one-half to full eye diameter anterior to lower eye; interorbital space very narrow, the vertical distance separating eyes less than half eye diameter; caudal peduncle present, its length 7.2–10.0 in HL; ventral edge of head posterior to mouth with 10–19 lappet-like cirri; edge of operculum at gill opening with slender well-spaced cirri on both sides; edge of lengthwise membranous ridges of dorsal and anal rays of ocular side with cirri, reduced and disappearing on about posterior half of fins; cirri also present on rays of blind side, but fewer and restricted to more anterior rays; lateral line aligned with dorsal edge of upper eye; upper end of gill opening in line with ventral fleshy edge of lower eye; anterior nostril reaching fleshy base of lower eye when laid back; caudal fin slightly pointed, its length 3.05–3.65 in SL; longest dorsal ray 1.4–1.8 in HL; anal rays and all but anterior dorsal rays of larger specimens branched

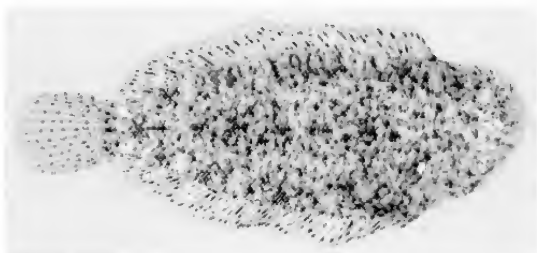


Figure 16. *Aseraggodes whittakeri*, BPBM 24113, 43.0 mm SL, Tutuila, American Samoa.

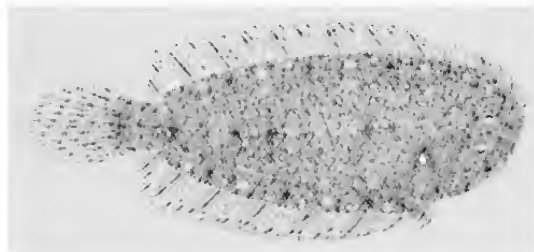


Figure 17. *Aseraggodes whittakeri*, ROM 64828, 42.0 mm SL, New Caledonia (R. Winterbottom)

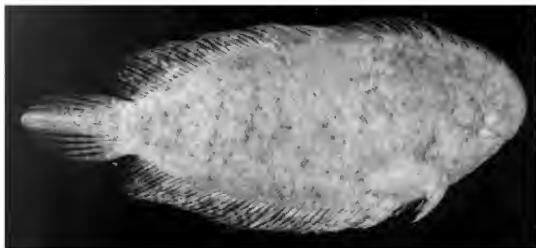


Figure 18. *Aseraggodes diringeri*, ROM 56917, 43.4 mm SL, Mayotte, Comoro Islands (R. Winterbottom).

distally; pelvic fins long, 1.65–1.85 in HL, the tip of longest ray extending to base of third or fourth anal ray; colour in alcohol of ocular side of most specimens pale tan without any dark markings; specimens from American Samoa with faint dark blotches in 3 rows on the ocular side, one row below base of dorsal fin, one along lateral line, and one above base of anal fin. Yellowish tan with many irregular pale markings partially outlined with dusky brown; fins pale with dusky specks

**Remarks.** Richard C. Wass recorded the brief colour note (above) on the label of the largest of three specimens, 43 mm SL, that he collected in American Samoa. A photograph of his specimen after 20 years in alcohol is presented as Figure 16. Figure 17 is a photograph of a fresh 42-mm specimen from New Caledonia taken by Richard Winterbottom. Most specimens of this species have an overhanging snout, the tip of the upper lip anterior and ventral to the lower lip, as shown in somewhat exaggerated form in the drawing of the holotype (Woods in Schultz et al., 1966: fig. 150). Unfortunately, Woods placed *Aseraggodes whitakeri* in the couplet of his key beginning with “snout not overlapping tip of the lower jaw”, and he wrote in his description, “snout not hooked over lower jaw.” He evidently confused this part of his description with that of *A. smithi* Woods. The dorsal-ray count of Woods is corrected from 72 to 76, and the anal-ray count from 51 to 52.

The drawing of the holotype is in error in the relative position of the eyes. The upper eye should overlap only about the anterior tenth of the lower eye. Also the dark blotches of the drawing are in the wrong positions. Those along the dorsal edge of the body should be 5 or 6 dorsal rays anterior to the position depicted. The largest dark blotch on the lateral line is also placed too posteriorly. It should be below the base of the fiftieth dorsal ray.

Wass (1984) reported three specimens from American Samoa. The largest, BPBM 24113, collected on the Taema Bank in 21.5 m, has only 3 rays in the right pelvic fin, a shorter base, and the left fin is shorter than normal. The other two specimens, BPBM 24130, from the same bank, but in 35 m, have normal pelvic fins.

The first specimen of this species was reported by Schultz (1943) from a channel at Hull Island, an atoll in the Phoenix Islands. He wrote, “it may be a specimen of *Aseraggodes melanostictus* (Peters).” The holotype was collected in 6 m from a lagoon coral head at Rongelap Atoll, Marshall Islands

by V.E. Brock and E.S. Herald in 1946. A second specimen from Micronesia was taken on a reef flat at Kapingamarangi Atoll in the Caroline Islands. The remaining specimens from the South Pacific are from the Chesterfield Bank in the Coral Sea and New Caledonia to the Society Islands. Depths of capture ranged from a tidepool at low tide in less than 0.2 m on the Chesterfield Bank to 37 m on the Taema Bank, American Samoa.

*Aseraggodes diringeri* Quéro, 1997 from the western Indian Ocean (type locality Réunion) has the same counts of fin-rays, lateral-line scales, vertebrae, and dorsal pterygiophores as *A. whitakeri*. It differs from *whitakeri* in its larger size. The holotype of *diringeri* measures 104 mm SL, and the one paratype is 59 mm in SL. Of 23 specimens of *diringeri* examined by the author, ten are larger than the largest *whitakeri* (43 mm SL). Judging from a single colour photograph of each species, the white markings of the body of *whitakeri* are nearly all vermiculate, as shown in Figure 17, whereas they are nearly all as discrete spots in *diringeri* (Fig. 18).

As noted in the two species accounts above, *A. whitakeri* is also similar to *A. pelvius* and *A. ramsaii*.

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## The species of *Dasyercus* Peters, 1875 (Marsupialia: Dasyuridae)

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### Abstract

Woolley, P.A. 2005. The species of *Dasyercus* Peters, 1875 (Marsupialia: Dasyuridae). *Memoirs of Museum Victoria* 62(2): 213–221.

Two species of *Dasyercus* (mulgaras) are recognised. They can be distinguished by the form of the tail, the number of upper premolar teeth in each jaw and, in the female, by the number of nipples in the pouch. *Dasyercus blythi* has a non-crested tail, two upper premolars (and a diastema between P<sup>2</sup> and M<sup>1</sup>) and six nipples; *D. cristicauda* has a crested tail, three upper premolars (the third very small and sometimes present on one side only) and eight nipples. Both species have a wide geographic range in the arid zone of Australia, and overlapping distributions. The identity of specimens previously referred to *D. cristicauda* in the W. B. Spencer collection of Museum Victoria has been reassessed and both species found to be represented.

### Keywords

Marsupialia, Dasyuridae, *Dasyercus blythi*, *Dasyercus cristicauda*

### Introduction

Four named forms of small carnivorous marsupials have been assigned to the genus *Dasyercus* Peters, 1875; three concern us here. The first was *Chaetocercus cristicauda* Krefft, 1867. Krefft's description was based on a single specimen sent to him by F. G. Waterhouse of the then Institute Museum of Adelaide (now the South Australian Museum). A second form, *Phascogale blythi* Waite, 1904, was described from specimens collected by A. C. Blyth in the Pilbara district of Western Australia. Two of Blyth's live animals had been left in the care of B. H. Woodward, Director of the Western Australian Museum and Art Gallery, and three were taken to Sydney, where E. R. Waite of the Australian Museum made observations on the live animals before returning them to Blyth, following which they escaped. Soon after, Woodward asked Waite to examine the remaining two specimens, expressing the wish that "if new, Mr Blyth's name might be associated with them". Woodward himself (1902) had mentioned them as "*Phascologale blythi*" without description, thereby erecting a nomen nudum. The third, *Phascogale hillieri* Thomas, 1905, was described from the skin of a specimen from Killalpaninna, South Australia, presented by H. J. Hillier.

Iredale and Troughton (1934) and Tate (1947) recognised two species of *Dasyercus*, namely *D. blythi* and *D. cristicauda* and these authors placed *D. hillieri* in the synonymy of *D. cristicauda*. Ride (1970) referred to only a single species, *D. cristicauda* and later Mahoney and Ride (1988) formally placed all three nominal species in the synonymy of

*D. cristicauda*. Consequently most authors have followed Ride. Mahoney and Ride included *Dasyuroides byrnei* Spencer, 1896 in the same genus but there is no consensus on the inclusion of *byrnei* in *Dasyercus*; *byrnei* is not considered here.

On the basis of unpublished information (received from M. Adams of the South Australian Museum) for the existence of two genetically distinct forms of *Dasyercus*, referred to as *D. cristicauda* and *D. hillieri*, *The 1996 Action Plan for Australian Marsupials and Monotremes* (Maxwell et al., 1996), listed *D. cristicauda* as "vulnerable" and *D. hillieri* as "endangered". Since then, in an unpublished report, Adams et al. (2000) have given their reasons for the names they applied to the two species. Further support for the existence of two genetically distinct forms of *Dasyercus*, based on gene sequences obtained from three whole mitochondrial genes (*cytb*, *12SrRNA* and *16 SrRNA*) has been obtained by M. Westerman and C. Krajewski (pers. comm.).

I first became aware of the existence of two distinct forms of *Dasyercus* when, in 1967, I collected specimens in south-western Queensland that differed from others that I had collected previously in the Northern Territory. The morphology of the tail clearly distinguished them as did the number of nipples in the pouch of females. There were also differences between the two forms in dentition. I maintained animals from both areas in captivity, and reported observations on the reproduction of animals from the Northern Territory (Woolley, 1971) and on the burrows made by animals from both the Northern Territory and Queensland (Woolley, 1990). The different sites reported for the burrows of the two forms suggest a difference



in their habitat requirements. Although I was aware of differences between animals from different localities, I followed Ride (1970) and referred to them as *D. cristicauda*.

Now that two forms of *Dasyercus* are again recognised, the discrepancy between the names applied by earlier authors (Iredale and Troughton, 1934; Tate, 1947) and those by Adams et al. (2000) warrants attention. In the present study, the type specimens of *Chaetocercus cristicauda*, *Phascogale blythi* and *Phascogale hillieri* have been examined and early literature reviewed. This was done to gain an understanding of the morphology of the three previously named forms and the reasons for them being considered to represent only two species. The reasons given for the use of the names *hillieri* and *cristicauda* for the two genetically distinct forms are then discussed. Because Spencer (1896) questioned the accuracy of Krefft's description of *Chaetocercus cristicauda*, the specimens studied by Spencer were examined to gain an understanding of his reasons. Specimens collected by me in south-western Queensland and the Northern Territory and thought to represent two species were compared with the types to establish their identities. Specimens in Museum Victoria (NMV), the Australian Museum (AM), the South Australian Museum (SAM) and the Western Australian Museum (WAM) have also been examined and they provide information on the distribution of the two species.

### The type specimens

*Chaetocercus cristicauda* Krefft, 1867. The holotype (AM M11342) is a mounted skin and skull (cranium and dentaries) of indeterminate sex. Krefft (1867) gave the following dimensions: total length 8 inches (203 mm), tail  $3\frac{1}{4}$  inches (82.5 mm), tarsi and toes  $1\frac{1}{8}$  inches (28.5 mm).

Krefft fitted the genus and species "upon a very singular animal, approaching in its dentition *Dasyurus* proper much more closely than any other known genus" [of the Dasyuridae], in reference to the reduction in the number of premolar teeth. In *Dasyurus* there are two upper and two lower premolar teeth. Key features of Krefft's description are: (i) the form of the tail, described as thick and compressed [i.e., having the two opposite sides nearly plane or flat] with a *crest of black hair upon the apical half* [my emphasis]; and (ii) the presence of three premolars in the upper jaw, the third being "diminutive and tubercular", and only two in the lower jaw. The general colour of the fur was described as leaden grey at the base, tipped with sandy and rufous, darker towards the tip. A colour plate accompanied the description and is reproduced here (Fig. 1a). The specimen was said by Krefft to be in not very good condition when it was received by the Museum, where it was mounted.

Examination of the holotype revealed that the mounted specimen bears little resemblance to the animal illustrated but part of the diagnostic crest of black hairs upon the apical half of the tail can be seen, and the hairs, at least on the head and back where the pelage has not been patched, are of the colour described, but are very much less rufous than depicted by the artist who prepared the colour plate. The compressed nature of the tail is not apparent because it appears to have been over-stuffed during preparation, and the left foot appears to be a

mismatched addition. The specimen was originally illustrated with the left foot partly obscured, perhaps because it was missing. All teeth ( $I \frac{1}{3}$ ,  $C \frac{1}{1}$ ,  $PM \frac{3}{2}$ ,  $M \frac{4}{4}$ ) have erupted in the holotype but some upper and all lower incisors have been lost. The right and left third upper premolars are present, and are small and tubercular as described by Krefft. Although it is unlabelled, I have no reason to doubt the association of the skull with the mount. It complies with Krefft's description, and in later studies by Iredale and Troughton (1934), Tate (1947) and Jones (1949), no doubts have been raised.

The type locality "South Australia, probably the neighbourhood of Lake Alexandrina" was considered doubtful by Jones (1949), "since *Dasyercus* is typically an inhabitant of the arid and semi-arid Centre and has since been obtained only from such environment, no specimen having been subsequently recorded from localities within 200 miles of the Coorong Lakes". Calaby (1996) expressed the same opinion, noting that Lake Alexandrina is "ecologically a most unlikely locality and almost certainly an erroneous one". Perhaps, in the absence of precise information from F.G. Waterhouse, who sent the specimen to him, Krefft may have seized on the comment "I hope soon to be able to send you some good skins of animals and some skeletons as my man is going to settle down near Lake Alexandrina . . .", made by Waterhouse in a letter dated 21 June 1895 (Archives of the Australian Museum C.20.65.21). In an earlier letter, 14 May 1865 (C.20.65.19), Waterhouse expressed disappointment that he had been unable to proceed, because of drought, on a trip from Port Augusta to Coffin Springs where he had hoped to trap some small mammals is suggestive of a more likely source area. Waterhouse said "I am convinced that the small marsupials and rodents of the northern part of South Australia are but little known – I know of several that are not described in Gould's work and I intend to do my best to procure them". Letters written by Waterhouse (held in the State Archives of South Australia) and by Krefft (held in the Mitchell Library, Sydney), even after the date of publication of the description, might yield information on where the specimen was collected.

Jones (1923) provided a very detailed description of the external characters of specimens of *Dasyercus* from Ooldea, South Australia collected by A.G. Bolam, referring to them as Krefft's Pouched Mouse, *Chaetocercus cristicauda*. Jones added some details to the description of the form of the tail. He noted that "The terminal half of the tail is ornamented with a large dorsal and a small ventral crest of shining black hairs. The ventral crest is inconspicuous, and consists of short stiff hairs which do not increase in length as they are followed towards the tip of the tail. The dorsal crest consists of long hairs which, starting as a mere ridge of fine black hairs, increases in length towards the tip of the tail and constitutes a fine fin-like crest." The 'inconspicuous' ventral crest may not have been obvious to Krefft (1867) because of the poor condition of the specimen upon which his description was based, or he may have overlooked it, as commented on by Spencer (1896: 22). Illustrations of the skull by Jones (1923, 1949) show three upper, and two lower, premolar teeth in each jaw. Jones also noted that the central area of the pads of the pes were striated and those of the manus, unstriated.

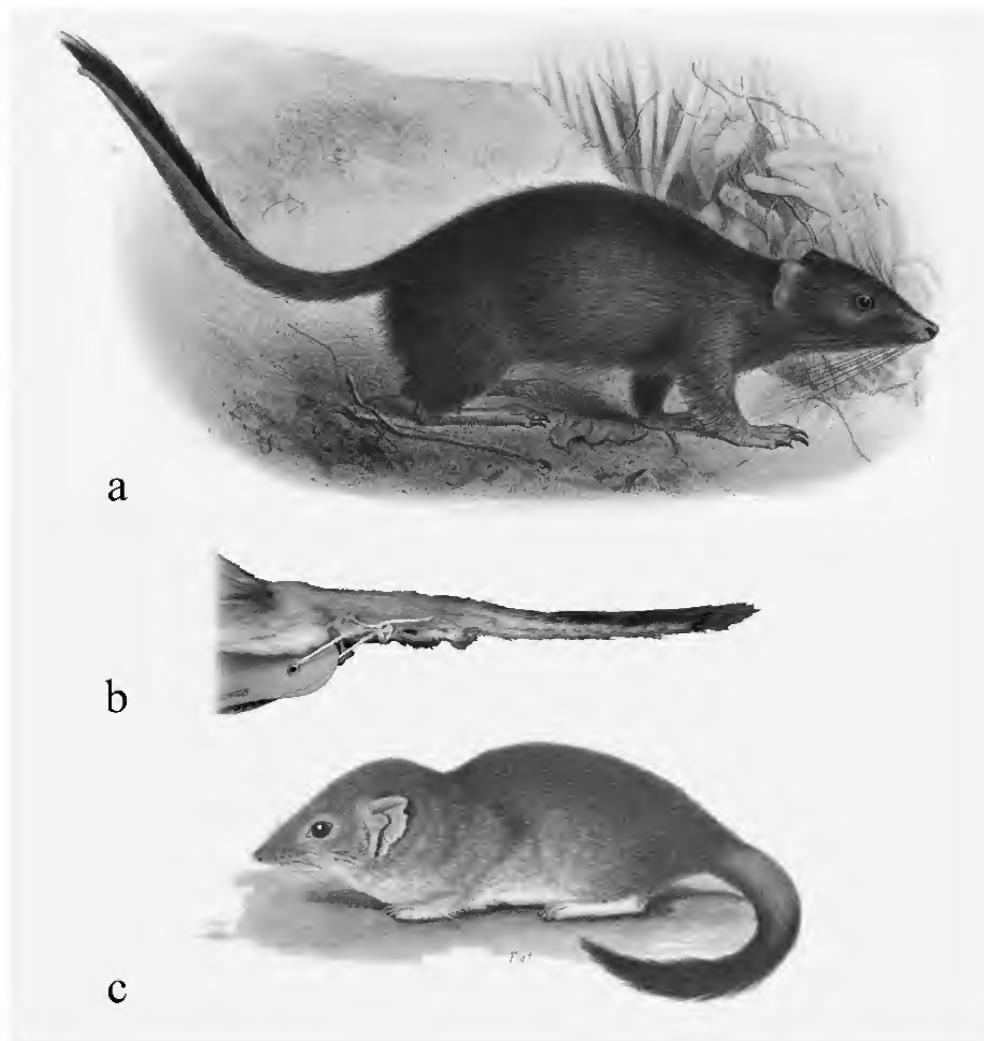


Figure 1. a, *Chaetocercus cristicauda* (= *Dasymercus cristicauda*) from Krefft (1866). b, tail of *Phascogale hillieri* Thomas, 1905 (= *D. cristicauda*) (photograph of type specimen © The Natural History Museum, London). c, *Phascologale cristicauda* (= *D. blythi*) from Spencer (1896).



Figure 2. Tails of *Dasymercus* species. a, *D. cristicauda* (NMV C5385). b, *D. blythi* (NMV C5340).

*Phascogale blythi* Waite, 1904. The syntypes, held in the Western Australian Museum, are mounted skins of a male M578 (renumbered M41476) and a female M579 (renumbered M41477), together with the skull (cranium only) of one bearing the label 'Type *Phascogale blighi* (Waite)', the nomen nudum introduced by Woodward. The dimensions of the specimens recorded by Waite (1904) were, for the male (adult); head and body 150 mm, tail 102 mm and hind foot 27.8 mm, and for the female (juvenile); head and body 132 mm, tail 95 mm and hind foot 26.5 mm. They were collected in the Pilbara region of Western Australia. Waite described the tail as: "... of moderate length, shorter than the head and body, incrassated; the proximal two-fifths above covered with short stiff yellow hairs, the remainder with gradually lengthening black hairs that *do not however form a crest* [my emphasis]. The whole of the lower surface is black, with the exception of a small proximal portion which is yellow." The colour of the pelage was given as "upper parts sandy, speckled with brown, the basal portion of the fur being dark grey and the whole of the under parts, together with the inner side of the limbs and the lining of the pouch is pure white". The footpads of both the fore and hind feet were said to be striated. He recorded various dimensions of the skulls of the two specimens, giving the 'basal length' of the skull of the male as 35.0 mm, and that of the female as 33.0 mm. Based on my measurement of the basicranial length (32.5 mm), the single skull now in the collection is probably that of the female. Details of the dentition are given. There are only two premolar teeth in the upper jaw, the first smaller than the second and, if as it appears that a superscript rather than a subscript has been used in error, two in the lower jaw. The lower premolars touch each other, and the first is in contact with the canine and the second with the first molar tooth. Jones (1949), without making specific reference to the apparent error, also interpreted this part of the description as a reference to the lower premolars.

Jones (1949) commented that Waite became acquainted with *Dasyercus cristicauda* during the time he was in charge of the Adelaide Museum (1914–1928), but never suggested that it was in any way akin to the Western Australian form that he had described in 1904.

*Phascogale hillieri* Thomas, 1905. The holotype is an adult male, skin without right hind foot and part of leg (Natural History Museum, London, no. 5.3.28.1). It was collected by H. Hillier at Killalpaninna, east of Lake Eyre, South Australia. Dimensions of the type (measured in the flesh): head and body 150 mm, tail 100 mm and hind foot 30 mm. The skull is lost.

Thomas (1905) considered the specimen to be "near *Ph. cristicauda*, but considerably paler in colour" [presumably by comparison with the colour plate accompanying the description by Kreff (1867)]. He described the tail as "slightly incrassated basally; *crested above for its terminal two inches* [my emphasis], the hairs attaining a length of 16 mm, nothing that can be called a crest below although some of the hairs are slightly longer than in the proximal part. In colour the main part of the tail is rather more rufous than the general body colour, though nothing like the corresponding part in *cristicauda*; under surface indistinctly darker, not black; crest glossy black".

Photographs of the holotype show the tail to be as described by Thomas (lateral aspect, Fig. 1b), and very like the tail of *D. cristicauda* described and illustrated by Kreff (1867) and Jones (1923). Dorsal fur colour of *D. hillieri* is similar to that of the type specimen of *Chaetocercus cristicauda* Kreff and thus only paler in reference to the colour plate.

On the morphological evidence, the type of *P. hillieri* cannot be distinguished from that of *C. cristicauda*. Iredale and Troughton (1934) therefore seem to have been fully justified in placing *P. hillieri* in the synonymy of *D. cristicauda*, a decision with which Jones (1949) agreed, having pointed out that in the intensity of coloration "*cristicauda* is a very variable animal, and that specimens that are considerably lighter in colour than usual are often captured with the more normal coloured individuals".

**Conclusion.** From the foregoing it is clear, based on morphological features, that there are two species of *Dasyercus*, namely *D. blythi* and *D. cristicauda*, as recognised by Iredale and Troughton (1934). The two are distinguishable by the form of the tail (not crested in *blythi*, crested in *cristicauda*), by the dentition (PM  $\frac{2}{2}$  in *blythi*, PM  $\frac{3}{2}$  in *cristicauda*) and to a lesser extent by their general body coloration (*blythi* a little less rufous than *cristicauda*). By association of their other morphological characteristics with those of the type specimens, for which nipple number was not available, the females of the two species can be distinguished by nipple number (six in *blythi*, eight in *cristicauda*).

### On the names of the genetically distinct forms

Adams et al. (2000) presented evidence for the existence of two clades using DNA sequence data for a small part of the mitochondrial gene *cytb* of 33 specimens of *Dasyercus* in museum collections. They were able to obtain DNA for sequencing from the type specimens of *Phascogale hillieri* and *Phascogale blythi*, but not from *Chaetocercus cristicauda*, and to establish that one clade includes the holotype of *hillieri* and the other, the syntypes of *blythi*. They presented a subset of the gene sequences of 171 base pairs from four specimens of each clade to illustrate the genetic differences between them.

Various morphological attributes of the 23 genetically typed individuals in the clade containing the type specimen of *hillieri* and the 10 in the clade containing the syntypes of *blythi* were then examined. They found that the two clades could be distinguished morphologically, the most diagnostic features being "crested on tail", distribution of hair on the pes and nipple number. Specimens in the clade containing the holotype of *hillieri* had uniformly long black hairs on the dorsal surface of the tail [which, by reference to illustrations in their report, means crested]; hairs from the outer side of the foot covering 33% of the sole, and seven or eight nipples. Those in the clade containing the syntypes of *blythi*, on the other hand, had black hairs covering most of the tail with the hairs increasing in length on the distal third [which, by reference to illustrations in their report, means non-crested], hairs from both sides of the feet covering 75% of the sole and six nipples.

Then, without any specific reference to the characteristic



features of the species given in the original descriptions, Adams et al. attempted to associate the type specimens with the specimens in each of their two clades. They stated, in reference to the clade containing the holotype of *hillieri*, "The cabinet skin of the holotype, *Phascogale hillieri*, appeared similar to the bodies (cabinet skins and spirit bodies) of animals referred to *Dasyercus hillieri* in Australian Museum collections. This diagnosis was fully supported by its DNA profile." Further, in reference to the clade containing the syntypes of *blythi*, "The cabinet skin of the holotype" [of *Dasyercus cristicauda*] "was referable to the bodies of animals assigned to *Dasyercus cristicauda* in this study." and "The cabinet skins of the holotypes, *Phascogale blythi*, are similar to the bodies of animals referred to *Dasyercus cristicauda*, a result consistent with the DNA profiles for both specimens."

The association of the name *hillieri* with one clade is supported by genetic evidence, "cresting on tail" and by the distribution of hair on the feet. Nipple number is not useful because it cannot be established in the holotype. However, the association of the name *cristicauda* with the other clade containing the syntypes of *blythi* has no support from either genetic or morphological evidence. Despite repeated attempts, DNA could not be extracted from the holotype of *cristicauda* and the tail of *cristicauda* is crested whereas that of *blythi* is non-crested. Distribution of hair on the pes and nipple number cannot be used in support of the association because these attributes cannot be assessed in the mounted type specimens of *cristicauda* and *blythi*. It is my conclusion that Adams et al. (2000) misplaced *cristicauda* in the clade containing the syntypes of *blythi*. The number of premolar teeth, a character not considered by them, differs and the tail of *cristicauda* has a crest like that of *hillieri*, which allies *cristicauda* with the clade containing *hillieri*. The correct name for specimens in this clade is therefore *D. cristicauda* (with which *hillieri* has been synonymised in the past) and, for the specimens in the other clade, *D. blythi*.

### Spencer collection

W. Baldwin Spencer, Professor of Biology at Melbourne University, was the zoologist on the Horn Expedition to Central Australia, May–August 1884. No *Dasyercus* were obtained in the course of the expedition but soon after Spencer started receiving specimens from friends. These post-Horn Expedition 'collectors' included P.M. Byrne of Charlotte Waters, C.E. Cowle of Illamurta and F.J. Gillen of Alice Springs. The real collectors were the Aboriginal people and precise localities where the specimens were found were not recorded. The exact number sent to Spencer is not known (Calaby, 1996) but 28 specimens (not including pouch young) of *Dasyercus* acquired between November 1894 and September 1895 can be found in the Spencer collection of Museum Victoria. Nineteen of the 28 were from Charlotte Waters, two from Crown Point and seven from Illamurta, all in southern Northern Territory.

Spencer (1896) identified them as *Phascologale cristicauda* Krefft, the Crest-tailed Phascologale, based on the "peculiarity of the dentition [a reference to the reduction in the number of premolar teeth], the crested tail and the general measurements

of the body." However, variability in form of the tail, dentition, nipple number and colour among the specimens he studied led him to give an amended description of the species (Spencer, 1896: 21–23).

Most of Spencer's specimens are intact (in spirit). The tail was examined and classed as either C (to denote the crested form of the tail of *D. cristicauda*) or B (the non-crested form of the tail of *D. blythi*). The dentition was examined in prepared skulls and intact specimens with particular reference to the upper third premolar tooth position (P = P<sup>3</sup> present, NP = P<sup>3</sup> not present, dP<sup>3</sup> = deciduous tooth in place). Tooth nomenclature follows Luckett (1993). Body measurements (total length, tail length and foot length in mm) of spirit specimens were taken, if not previously recorded. The reproductive status of individuals was assessed by examination of the pouch area and reproductive organs of both females and males. Females were assessed as mature if they were lactating or showed signs of having reared young previously (nipples elongated, pouch fur stained), or, in one case, the appearance of the uteri indicating that the individual had very recently given birth. Nipple number was determined in most immature and mature females. Males were assessed as mature if the scrotum was large and the prostate gland developed and showing zonation. The size of the scrotum alone is not a good indicator of maturity because development of the prostate occurs after the testes have reached full size.

Two species of *Dasyercus* can be recognised (Table 1), five specimens (four from Charlotte Waters and one from Crown Point) of *D. cristicauda* (crested tail, P<sup>3</sup> present) and 23 of *D. blythi* (non-crested tail, P<sup>3</sup> not present). This agrees with the Spencer's (1896) observation that P<sup>3</sup> was absent in most of his specimens. Females identified as *D. cristicauda* have eight nipples and *D. blythi* have six. None was found to have four nipples as reported by Spencer; he may have overlooked very small, unsucked nipples in the pouch of lactating females. In this sample, specimens of *D. cristicauda* are larger than *D. blythi*; two mature males of *D. cristicauda* having head-body lengths of 180 and 185 mm and foot length of 33.5 mm, and two *D. blythi* with a head-body length of 135 mm and foot lengths of 26.5 and 27.5 mm. In both species tail length is less than head-body length. I was unable to distinguish between the pads of the manus of the two species (said to be unstriated in *D. cristicauda* and striated in *D. blythi*) but in this long preserved material it was difficult to see striations on any pads.

Spencer (1896) failed to recognise that the variability he saw could be accounted for by two species. The specimen that he illustrated, as *Phascologale cristicauda* (Fig. 1c), has the tail of *D. blythi*. A skull of a specimen from Charlotte Waters (C.6158, not included in Table 1), is labelled in Spencer's hand "Fig. spec." It has the characteristics of *D. blythi* (ie P<sup>3</sup> absent, diastema between P<sup>2</sup> and M<sup>1</sup>) and may be the missing skull of C.5388 (see Table 1). If so, specimen C.5388 would be the specimen illustrated. The tails of the two species are illustrated in Fig. 2 and dentition in Fig. 3.

In a further 120 specimens, identified as either *D. blythi* or *D. cristicauda* on the form of the tail, P<sup>3</sup> was absent from all specimens of *D. blythi* except one (SAM M3115).

Table 1. Data for 28 specimens of *Dasyercus* from Charlotte Waters, Crown Point and Illamurta held in the Spencer collection, Museum Victoria. See text for explanation of assessment of reproductive status, form of the tail (B = *D. blythi* and C = *D. cristicauda*) and P<sup>3</sup>.

Reg. no. C	Accession date	Specimen	Sex	Reproductive status	Form of tail	No. of nipples	P <sup>3</sup>	H-B mm	Tail mm	Foot mm
Charlotte Waters (25°55'S, 134°56'E)										
234	23.3.1916	spirit, skull	♀	mature	B	6	NP	—	75	24.5
5336	—, 9.1895	spirit	♀	mature	B	6	NP	130	85	24.5
5337	—, 12.1894	spirit	♀	mature	B	6	NP	125	85	25.5
5338	—, 9.1895	spirit	♀	mature	B	6	NP	130	80	25.0
5339	—, 9.1895	spirit	♀	mature	B	6	NP	125	85	24.0
5340	—, 9.1895	spirit	♂	mature	B	—	NP	135	100	26.5
5359	—, 2.1895	spirit	♀	mature	B	6	NP	130	75	23.5
5360	—, 2.1895	spirit	♀	weaner	B	—	dp <sup>3</sup> *	85	45	19.5
5361	—, 2.1895	spirit	♂	immature	C	—	P	125	85	25.5
5369	—, 2.1895	spirit	♀	mature	B	6	NP	125	85	24.5
5370	—, 2.1895	spirit	♀	mature	B	6	NP	130	70	25.0
5371	—, 12.1894	spirit	♀	mature	B	6	NP	120	80	23.5
5372	—, 2.1895	spirit	♀	immature	B	6	NP	115	75	25.5
5384	18.12.1895	spirit	♀	mature	B	6	NP	130	90	26.0
5385	18.12.1895	spirit	♂	mature	C	—	P	180	110	33.5
5387	1895	spirit	♀	weaner	B	6	dp <sup>3</sup> *	80	50	19.5
5388	1895	spirit (—head)	♀	mature	B	6	—	—	80	26.0
5391	1.7.1895	spirit	♀	immature	C	8	P	155	100	30.5
5392	—, 7.1895	spirit	♂	mature	C	—	P	185	120	33.5
Crown Point (25°30'S, 134°23'E)										
5357	—, 8.1895	spirit	♀	mature	C	8	P	150	100	30.5
5358	—, 8.1895	spirit	♂	mature	B	—	NP	135	95	27.5
Illamurta (24°18'S, 132°41'E)										
4828	—, 11.1895	spirit	♀	immature	B	6	dp <sup>3</sup> (L)	75	65	23.0
4829	—, 11.1895	spirit	♂	immature	B	—	dp <sup>3</sup> (R)	105	70	25.0
4830	—, 11.1895	spirit	♂	immature	B	—	NP	105	65	24.5
4831	—, 11.1895	spirit	♂	immature	B	—	dp <sup>3</sup> (L)	100	70	23.0
5362	4.10.1895	spirit (—gut)	♂	—	B	—	NP	150	90	27.0
5380	16.11.1894	spirit (—tail)	♂	immature	B	—	dp <sup>3</sup>	90	65	21.5
5381	16.11.1894	spirit (—tail)	—	immature	—	—	NP	—	—	21.5

\*not erupted – gum previously cut to expose the tooth

A characteristic feature of *D. blythi* is the presence of a diastema between P<sup>2</sup> and M<sup>1</sup> in mature specimens. P<sup>3</sup> was present in both mature and immature specimens of *D. cristicauda* with the exception of two mature specimens (SAM M3106, M3154). These three aberrant individuals formed part of a collection from the Canning Stock Route (Table 2), which raises the possibility that the skins and skulls of two (M3106 and M3115, both with adult dentition) were mismatched, but provides no obvious explanation for the absence of P<sup>3</sup> in the mature specimen (M3154). However, the teeth of this specimen were very worn, and the rough appearance of the bone between P<sup>2</sup> and M<sup>1</sup> suggested that P<sup>3</sup> might have been lost. In specimens of *D. blythi* the deciduous third premolar was found unerupted (Table 1) in 'weaners', young close to independence in which all upper incisor teeth except the first pair had erupted. The eruption of I<sup>1</sup> later than the other incisor teeth is thought to be an adaptation for suckling (Luckett and Woolley, 1996). Deciduous premolar teeth were seen in some immature

individuals of *D. blythi* (Table 1), and *D. cristicauda* (e.g., SAM M19672, M20913 and M20925) and the right dp<sup>3</sup> was seen in a mature *D. blythi* (SAM M3146).

### Woolley specimens

Specimens collected on Sandringham Station, south-western Queensland (Woolley, 1990) have features characteristic of *D. cristicauda* (Western Australian Museum, M8207, M9670-73, M13716; Queensland Museum, JM5532). Specimens collected in the vicinity of Papunya, near Uluru, on the old Docker River Road west of Uluru, and near Refrigerator Well, Tanami Desert, all Northern Territory (see Woolley, 1990 for details of localities) have features characteristic of *D. blythi* (Museum Victoria, Uluru, C35885, C35886; Papunya, C35887–C35895; Tanami Desert, C35896, C35897; Queensland Museum, Docker River Road, JM1443; Tanami Desert, JM2311, JM2312, JM2317).

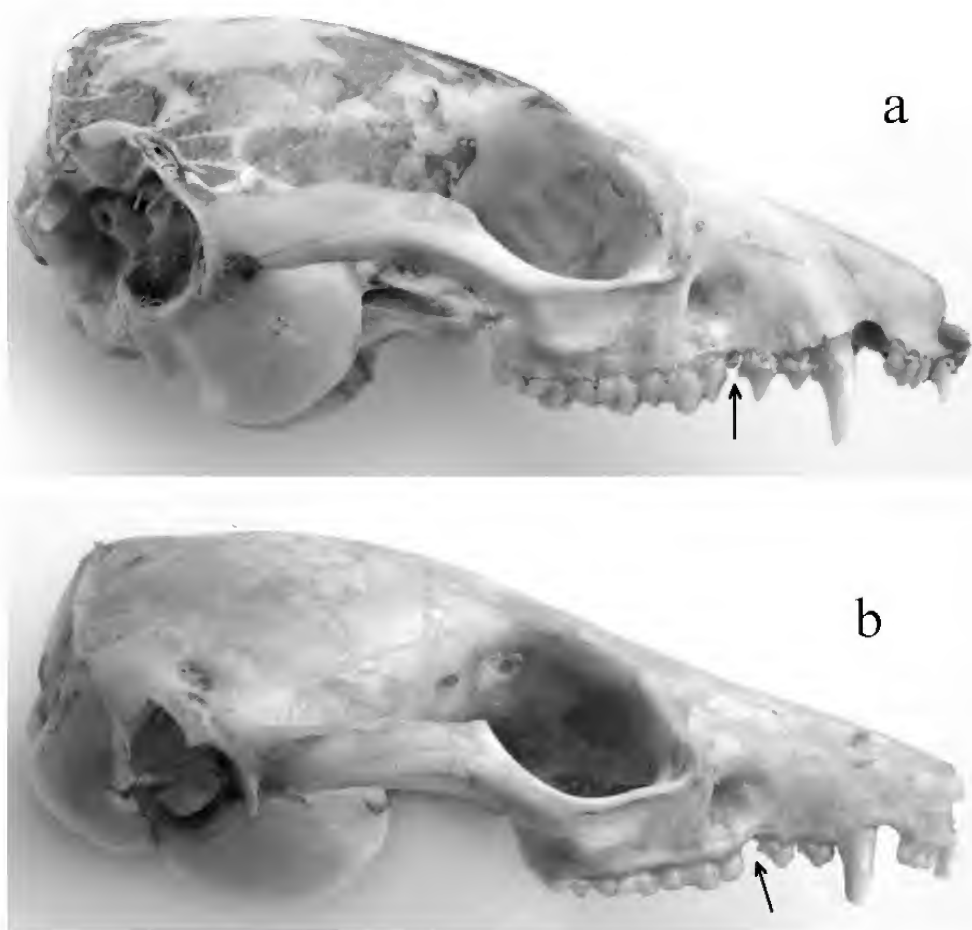


Figure 3. Lateral view of the skulls of *Dasymercus* species. a, *D. cristicauda* female (NMV C676), showing P<sup>1</sup> (arrowed). b, *D. blythi* female (NMV C234), showing the diastema (arrowed) between P<sup>2</sup> and M<sup>1</sup>.

### Distribution

*Dasymercus* has a wide distribution across the arid zone of Australia (see maps in Woolley, 1995 and Australian Mammal Map Updates at <http://www.naturebase.net/science/mupdates.html>). The past and present distribution of each species requires clarification to assess their conservation status. Of the many museum specimens available, those from two areas at the species' north-western and south-western limits have been examined, in addition to those above from central Australia in the Spencer collection.

**Canning Stock Route.** Otto Lipfert, taxidermist of the Western Australian Museum, accompanied the Canning Stock Route Expedition of 1930–1931 through the north of Western

Australia. Twenty-four specimens collected by him and lodged in the South Australian Museum have been examined (Table 2). Based on the form of the tail, 13 were identified as *D. cristicauda* and 11 as *D. blythi*. The specimens were collected along the Stock Route, from Well 27 to Well 49, and both species were found in the vicinity of Wells 27, 35 and 45. Lipfert reported that he collected specimens up to 2–3 miles from well sites (McKenzie and Youngson, 1983). An indication that the two species may occupy different habitats comes from the collector's notes on two specimens: *D. cristicauda* M3107 – “top of sandhill” and *D. blythi* M3144 – “spinifex flat”. The annotated map of the Stock Route accompanying the article on Mr Canning's Expeditions in Western Australia 1906–1907 and 1908–1910 (Anon, 1911) shows the positions of the wells and



Table 2. Data for 24 specimens of *Dasyercus* from the Canning Stock Route held in the South Australian Museum. Explanation as for Table 1. \* aberrant specimens referred to in text

Well no. (coordinates)	Reg. no. M	Date	Specimen	Sex	Reproductive status	Form of tail	No. of nipples	P <sup>3</sup>
27 (22°48'S, 123°39'E)	3140	–.7.1930	spirit, skull	♀	immature	B	6	NP
“	3141	–.7.1930	skin, skull	♀	–	C	–	P
28 (22°39'S, 123°45'E)	3142	–.8.1930	spirit	♀	mature	C	8	P
29 (22°34'S, 125°53'E)	3143	–.8.1930	skin, skull	♀	–	C	–	P
“	3144	–.8.1930	skin, skull	♀	–	C	–	P
“	3154*	–.8.1930	spirit, skull	♂	mature	C	–	NP
33 (22°20'S, 124°44'E)	3145	–.10.1930	skin, skull	♂	–	B	–	NP
34 (22°16'S, 124°54'E)	3146	–.10.1930	spirit, skull	♀	mature	B	6	dp <sup>3</sup> R
35 (22°13'S, 125°03'E)	3105	29.10.1930	skin, skull	♂	–	C	–	P
“	3147	–.10.1930	skin, skull	♀	–	B	–	NP
“	3148	–.10.1930	skin	♂	–	B	–	–
36 (22°08'S, 125°17'E)	3106*	5.11.1930	skin, skull	♂	–	C	–	NP
“	3149	–.11.1930	skin, skull	♀	–	C	–	P
41 (21°33'S, 125°51'E)	3107	4.6.1931	skin, skull	♂	–	C	–	P
“	3150	–.6.1931	skin, skull	–	–	C	–	P
42 (21°19'S, 125°53'E)	3108	24.5.1931	skin, skull	♂	–	B	–	–
43 (21°12'S, 125°54'E)	3109	17.5.1931	skin, skull	♂	–	C	–	P(L)
44 (20°02'S, 126°04'E)	3110	2.5.1931	skin, skull	♂	–	C	–	P
45 (20°48'S, 126°11'E)	3111	6.5.1931	skin, skull	♀	–	C	–	P
“	3112	18.4.1931	skin, skull	♀	–	B	–	NP
“	3113	19.4.1931	skin, skull	♂	–	B	–	NP
“	3114	18.4.1931	skin, skull	♂	–	B	–	NP
47 (20°26'S, 126°18'E)	3115*	1.4.1931	skin, skull	♂	–	B	–	P
49 (20°10'S, 126°41'E)	3117	2.3.1931	skin, skull	♀	–	B	–	NP

Table 3. Data for 13 specimens from Ooldea, Fisher and Rawlinna held in the Australian Museum. Explanation as for Table 1. \* Too young for P<sup>3</sup> to have erupted. (I<sup>1</sup> not erupted in M4923; partially erupted in others).

Locality	Reg. no. M	Date	Specimen	Sex	Reproductive status	Form of tail	No. of nipples	P <sup>3</sup>
Ooldea (30°27'S, 131°50'E)	2987	12.8.1921	skin, skull	♂	–	C	–	P
“	2988	12.8.1921	spirit, skull	♂	mature	C	–	P
“	3025	29.8.1921	spirit, skull	♂	mature	C	–	P
“	4923	23.10.1921	spirit	♂	immature	C	–	*
Fisher (30°33'S, 130°58'E)	4862	22.10.1921	skin, skull	♂	–	C	–	P
“	4863	23.10.1921	skin, skull	♀	mature	C	–	P
“	4864	23.10.1921	skin	♀	mature	C	8	–
“	4865	23.10.1921	skin, skull	♂	immature	C	–	*
“	4866	24.10.1921	skin, skull	♀	immature	C	–	*
“	4924	24.10.1921	spirit	♀	immature	C	8	*
“	31546	20.10.1921	spirit	♀	mature	C	–	P
Rawlinna (31°01'S, 125°20'E)	4355	30.7.1928	spirit, skull	♀	mature	C	8	P
“	4356	30.7.1928	skin, skull	♀	–	C	–	P

gives details of the country traversed, which includes a mixture of spinifex flats and sand-ridge country.

*Ooldea, Fisher, Rawlinna.* These localities are near the south-western limit of the distribution of *Dasyercus*. It was from Ooldea that Jones (1923) obtained his specimens of *D. cristicauda* but his material has not been located. Thirteen specimens (four from Ooldea, seven from Fisher and two from Rawlinna) held in the Australian Museum have been identified as *D. cristicauda* based on the crested tail, presence of P<sup>3</sup> in mature specimens and eight nipples in females (Table 3).

Remarks by Bolam (1925) suggest that *D. blythi* may also occur in the area. He wrote (p. 25) “This animal [the Crested-tailed phascogale], which bears the scientific name of *Dasyercus cristicauda*, is known to the blacks as Mul-gurra. Two species of the Phascogale family are found on the Nullarbor Plain and the sandhills of Ooldea. These are the Crested-tailed and the Brush-tailed; but with the exception of a *small difference in the hair on the tail the species are alike in appearance and habits*” [my emphasis].

The presence of the two species, *D. cristicauda* and *D. blythi*, in central Australia (the Spencer collection) and

north-western Australia (the Canning Stock Route collection) together with the possibility that both may be found in the south-western limit of the range (Ooldea/ Nullarbor Plain), suggests that the two could occur throughout much of the range.

### Common names

Mulgara, the name by which *Dasyercus cristicauda* was known to the Aboriginal people at Ooldea, has been used as its common name. Spencer (1896) knew that the Aborigines at Charlotte Waters and Illamurta used the name Amperta but it is impossible to know to which of the two species this might have applied. Many Aboriginal names for *Dasyercus* have been recorded by Finlayson (1961) and Burbidge et al. (1988), one of which, Ampurta, has been used as the common name for *D. hillieri*, here no longer recognised as distinct from *D. cristicauda*. With his recognition of two species, Troughton (1965) referred to them as the Crest-tailed Marsupial Mouse (for *D. cristicauda*) and the Western Crest-tail (for *D. blythi*). The latter common name is inappropriate because *D. blythi* is not restricted to the western part of the range, and it does not have a crested tail. Because Mulgara was a familiar common name for *Dasyercus* when it was thought by some to be a monotypic genus I propose that it be retained; with *D. blythi* to be known as the Brush-tailed Mulgara and *D. cristicauda* as the Crest-tailed Mulgara. Both species have black hairs on the distal half of the tail but the dorsal, fin-like crest of *cristicauda* provides a simple means of differentiating between the two species in the field.

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